

The American Midland Naturalist

Founded by J. A. Nieuwland, C.S.C.

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The AMERICAN MIDLAND NATURALIST is a general biological periodical published quarterly by the University of Notre Dame. It welcomes to its pages articles of a descriptive, analytical, and experimental nature. Review articles on topics of current interest in the various fields of Biology are also welcome.

Subscription rate per year \$10.00 in the U. S., Mexico, and South American countries; \$11.00 elsewhere.

Address All Correspondence to:

AMERICAN MIDLAND NATURALIST
University of Notre Dame
Notre Dame, Indiana

© 1961, University of Notre Dame Press.

Entered as second-class matter at Notre Dame, Indiana. Accepted for mailing at special rate of postage provided for in Section 1103; Act of October 3, 1917, authorized on July 3, 1918.

Theodor Karl Just
1904-1960



Theodor Karl Just, 1904-1960

When Theodor Karl Just died on 14 June 1960 at his home in Oak Park, Illinois, the world of science, and of men, was deprived of a unique person. It was the end of a life of a scientist, and of a man, who devoted more time to the work of others, and to them, than he did to his own work, or to himself.

He was born in Gross Gerungs, Austria, on 27 October 1904. His mother was Anna Traindl. His father, Alois, whose avocation was the ecology of the region, was a teacher who became superintendent of the school system of Krems, Austria, 40 miles west of Vienna. Judged by its products, the household was a scholarly, cultured one, for there were three sons—one a physician, one a Ph.D. in music, and one, the botanist Ted Just, who, in everything and to everyone, demonstrated gentility, an appreciation of the arts, sincere interest in other persons, and continuous devotion to selfless scholarship.

His boyhood interest in natural science, fostered by his father's own interest in it, developed into a career in botany. He obtained the Ph.D. at the University in Vienna in 1928. For the year following, he was an assistant in the herbarium at the Museum of Natural History in Vienna.

In his last year at the University in Vienna, he became the friend of Rev. F. J. Wenninger, C.S.C., who was studying there. Father Wenninger, head of the Department of Biology and Dean of the College of Science at the University of Notre Dame, was one of the important people in Dr. Just's life. He persuaded Dr. Just to join the faculty of Notre Dame. In 1929 he came as Instructor in Biology and Curator of Botanical Libraries and Herbaria. He remained at Notre Dame for seventeen years. During these years, he matured as a scientist, editor, and administrator, and formed lasting associations with the University. He was instructor from 1929 to 1933, Assistant Professor to 1936, Associate Professor to 1941, Professor to 1945, and J. A. Nieuwland Research Professor in Botany from 1945 to 1946, when he resigned to go to the Chicago Natural History Museum. At the Museum he was Chief Curator of the Department of Botany from 1947 until shortly before his death.

At the death of Father Wenninger in 1940, he was appointed head of the department, and held this post during the difficult years of the war. He brought the best of the European scientific tradition to his job as department head. He visualized a department representing both experimental and non-experimental Biology (*i.e.*, no emphasis on one at the sacrifice of the other). In this atmosphere he believed that a student could develop a broad outlook and gain a general appreciation of Biology and its relation to other scientific disciplines under the guidance of a staff who were contributing to knowledge in their fields of interest. Because of the unusual teaching demands caused

by the war, balanced progress was not easy. And, finally, the enormous amounts of time required by his other activities forced him to choose in favor of the Chicago Natural History Museum, where he could devote time to his other interests. In the five years as head of the department, he made a lasting impact, and a solid contribution to the University. During this time, despite the difficulties of maintaining and building a staff, he saw the department become a lively teaching and research center. While at the Museum in Chicago he continued his university associations as Research Associate in the Department of Biological Sciences at Northwestern University, and as Professorial Lecturer in the Department of Botany at the University of Chicago. From 1938 he was also Scientific Director of the Lloyd Library of Botany, Pharmacy, and Materia Medica in Cincinnati, Ohio.

One of his outstanding characteristics was his interest in scientific accomplishment itself, and the pride he could take in the role of others in it. So it is appropriate, and perhaps a required consequence, that probably his greatest permanent influence was effected through his activities as an editor. Upon his arrival at Notre Dame, he made a second important friendship — that with Father J. A. Nieuwland, the chemist and botanist. Father Nieuwland persuaded Dr. Just to be assistant editor of *The American Midland Naturalist*, a small journal devoted to the natural history of the region, and he was its editor from 1935 until 1946. With his friend, Prof. J. H. Hoskins of the University of Cincinnati, he founded the journal *Lloydia* in 1938 and was its first editor.

Through the pages of *Lloydia* in his score of years as Editor have come a variety of articles each attesting to his successful efforts to implement the flow of scientific information.

From 1940 he was an assistant editor of *Chronica Botanica*. He also edited such publications as "Plant and Animal Communities" in 1939, and a series of monographs from 1944 to 1946.

The monographs appeared as Nos. 1, 2 and 3 in *The American Midland Naturalist Monograph* series. The establishment of this series during the period of the Second World War was fraught with problems other than those usually thought of as editorial. A perusal of the correspondence attendant to the publication of the first monograph reveals his optimism when confronted with paper shortages and delay due to lack of printing facilities and personnel. In founding this series, he provided one of the few outlets in this country for publishing longer manuscripts.

His roles in founding *Lloydia* and *The American Midland Naturalist Monographs* are clear. Not so obvious is his contribution to the development of *The American Midland Naturalist*. He set out to broaden its scope, both in content and in geographical influence, and he succeeded. At the beginning of his editorship he made it almost a one-man task, functioning as editor and publisher, spending many hours at his editorial desk or in the printshop. His editorial function sometimes included reworking manuscripts almost to the point of complete rewriting. In this way he was directly, but anonymously, respon-

sible for the production of excellent scientific papers that, without his work, would have been something less, or perhaps would not have existed. He believed it his duty to become personally and intimately involved as much as necessary to produce the best possible paper if the material offered was good, and it probably never occurred to him to reject a paper containing substantial observations and ideas just because it was badly prepared, and would mean countless hours of work for him. In performing these duties, he was living his beliefs that he described when he wrote that editors "must function as public servants creating the all-important liaison between contributor and reader through the medium of their journal . . ." and that "they work for the benefit of the maximum number of people and the advancement of science." It is apparent that he considered his editorships as an important life purpose, and that he fulfilled this purpose zealously. He insisted that his friend Father Nieuwland be given prominent credit for founding *The American Midland Naturalist*; we can insist that Dr. Just be given credit for making it an important scientific journal.

His chief contributions to botany and paleobotany stemmed from his ability to synthesize literature, to prepare up-to-date reviews or summaries, and to prepare publications and promote research. His articles were skilfully written and generally "covered the field" with careful balance. Such articles as "Progress in Paleobotany, 1908-1958," "Fossil Floras of the Southern Hemisphere and their Phytogeographical Significance," "Gymnosperms and the Origin of the Angiosperms," "The Rates of Evolutionary Processes," "Pharmacopoeias, Dispensatories, Formularies and Allied Publications," and "Geology and Plant Distribution," indicate his wide interests and breadth of comprehension. These and similar writings, though each is usually but a few pages long, are comprehensive syntheses of the literature.

In botany, Dr. Just's writings were concerned largely with summarizing the history of ideas, resolving confusion in terminology, taxonomy and morphology, encouraging and summarizing ecologic studies and his study of certain members of the Chenopodiaceae. A most important botanical contribution was his encouragement of many professional botanists and students to write up their ideas, to engage in certain types of research, to study certain problems, and to translate important foreign works. To many of these works or writings, he made direct contributions, usually known only to the author or researcher whom he was encouraging. This influence often took the form of precise advice, suggestions, bibliography, translations, re-writing of manuscripts, suggesting names, clarifying rules of taxonomy and nomenclature, obtaining funds or publication media, or introducing botanists to one another. He was responsible for helping numerous botanists find a locale or institution receptive to their work, and for bringing a number of people together for collaborative studies.

Paleobotany was a challenging field of interest which gave Dr. Just a satisfying diversion from his editorial routine and his botanical reading and writing. His fundamental concern for paleobotany developed in his long association with Professor Hoskins of the Univer-

sity of Cincinnati. Hoskins, a student of Chamberlain at Chicago, was keenly interested in plant morphology. It was a similar interest in Dr. Just's repertoire that afforded the plane on which their lifelong friendship first developed. "Doc" and "J.H.," as they always called each other, made a point of getting together two or three times a year. They took a number of field trips together during their earlier years. Typical of these were botanical trips to bogs and swamps of Indiana and Michigan, and forays to such botanically unique or interesting spots as "Tight Holler" or Natural Bridge, Kentucky.

Their paleobotanical trips were numerous, including one memorable trip, in the summer of 1941, to many of the principal fossil plant localities in western United States. There, in company with Aural T. Cross and Arthur H. Blickle, they visited Iowa coal-ball localities; climbed to the "Mecca" of American paleobotanists, the gigantic fossil *Sequoia* stump high up on the side of Specimen Ridge in Yellowstone Park; tramped the arid country of the John Day beds in Oregon; searched for *Tempskya* along pioneer overland trails in southwestern Wyoming; "scratched" for cycads below the crest of the Dakota and Lakota hogbacks above the "racetrack" in the Black Hills area; probed for petrified *Ginkgo* wood in the lava flows of the Columbia River in Washington; and hammered on the mid-Devonian channel fill at Beartooth Butte for *Psilophyton*.

Dr. Just was not physically powerful, but he was enthusiastic and persevering in the rough field work, and he thoroughly enjoyed the accompanying camping routine. On these excursions he constantly "taught" his companions the latest in morphology, often from some of the most obscure foreign publications, or discoursed at length on taxonomic and nomenclatorial matters to the extent that one student was heard to remark, "This trip sounds like a plenary session of the Roman Senate!"

Dr. Just made important contributions to general paleobotanical literature and American paleobotany. He developed several review papers which were exceptionally scholarly in organization and valuable for broad coverage. He was in the forefront of the work of the Paleobotanical Section of the Botanical Society of America, serving several years as secretary and later as chairman. He also represented that organization on the Editorial Board of the *American Journal of Botany* and brought together three extensive summaries of activity and bibliographies of paleobotanical work in the country, the last of which, for the years 1952-1957, was published in *Lloydia* after his death.

He had become quite interested in the Mesozoic flora during the last ten years of his life and studied the broader aspects of the morphology and evolution of the cycads and their relationship, along with other gymnosperms, to the primitive angiosperm stocks. He designed and supervised the construction of some very remarkable exhibits of cycadeoid plants at the Chicago Natural History Museum.

One of Dr. Just's most remarkable characteristics was his extensive knowledge of biological literature, both in books and journals. He was a proficient linguist and seemed to delight in scanning books and articles in any of several languages and then give his friends lucid

summaries of these at late night coffee meetings or afternoon "tea-breaks." His more than 150 published "Reviews," most of them of extensive treatises or books, represented only a small portion of those he read and then discussed with his colleagues. The authors of many manuscripts which were submitted to him for publication in *The American Midland Naturalist* or in *Lloydia*, learned of the tremendous scope of his knowledge of the literature when they received his suggestions concerning their bibliographies.

On the national and international level, he discharged many society and committee duties. At times, he was Vice-President and President of the Indiana Academy of Science, Secretary to the Paleobotanical Section of the Botanical Society of America, Chairman of the Committee on Paleobotanical Nomenclature of the same section, Secretary and Vice-President of the Society for the Study of Evolution, Chairman of the Committee on Paleobotany of the National Research Council, Chairman of the Committee on Editorial Policy of the Conference of Biological Editors, and Vice-President of the Conference. The last activity was a significant one to him in the last part of his life. During the war he was consultant to the Office of Strategic Services.

As most of us, Dr. Just had many cares. Especially important to him were the welfare of his mother and his two brothers (one killed in an air raid) during the war; the deaths of his friends Father Nieuwland, Father Wenninger, Dr. Lyon, and Professor Hoskins; the unfortunate misunderstandings arising from certain administrative decisions that always were honorably motivated; his grief for his young family as he lived out his last months with certain knowledge of his imminent death. Unlike most of us, however, he kept his cares to himself. Only a few — and perhaps only one — of his friends appreciated his burdens. To most people, Dr. Just was friendly, warm, affable, smiling, able and helpful, a botanist and editor that we sought out, for he helped us with our difficulties and never troubled us with his. One who was privileged to talk with him on the brink of his death saw Ted Just as he always had been, talking of *Lloydia*, manuscripts, science (he furnished a reference), children, and of how we must get together soon for an evening of Hugo Wolf and Schubert — with flute, piano and voice, as we did many years ago.

What were the important things in his life? Professionally — his broad interest in biology, his sincere, unselfish concern for biologists and their development and progress, his frank admiration of scholarship, his association with the University of Notre Dame, and, most important, perhaps giving him more satisfaction and sense of accomplishment than any other, the "Midland" which is his memorial. Personally — his numerous friends and the warm relationships he had with them, and his temporal source of solace and strength, his wife and three daughters. His home was the center of his life. One saw the best of a good man there. *Requiescat in pace.*—A. T. CROSS and E. L. POWERS.

PUBLICATIONS OF THEODOR KARL JUST*

1930

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1931

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* We are indebted to Dorothy Gibson and Lillian A. Ross of the Chicago Natural History Museum for their kind assistance in the preparation of this bibliography—EDITOR.

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The American Midland Naturalist

Published Quarterly by The University of Notre Dame, Notre Dame, Indiana

Vol. 65

APRIL, 1961

No. 2

A Study of Homing in the Cotton Mouse, *Peromyscus gossypinus*

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ABSTRACT: Homing success of animals released in unnatural habitat (golf course) adjacent to their home area was less than in natural areas at comparable distances. In natural areas, males homed with greater success than females from distances greater than 500 feet. In unnatural areas there was no sex difference. Initial orientation in unfamiliar territory could not be correlated with the direct route home. The distance of the homesite from the release area (1000 feet to 60 miles) apparently did not influence initial orientation. Repetitive liberations of successfully homing mice from the same release site on the golf course indicated that mice can learn homing pathways. Mice which had homed a number of times and were then held in captivity for periods of more than 12 weeks before being liberated at former release sites showed no decline in their homing ability. Animals released in their former home ranges occupied prior to extended periods of laboratory isolation remained and maintained these areas. Animals without previous experience from artificial displacement returned to and maintained their former home ranges when released at various distances from their capture sites after prolonged laboratory isolation. The results indicate that cotton mice are capable of learning and retaining for prolonged periods of time a schema of their environment and are able to utilize this information in homing activity.

It is postulated that psychological factors are the principal source of motivation to home. Based on the degree of psychological attachment to an area small rodents may have three types of zones: 1) Territory; 2) Home range; and 3) Life range. The latter is considered to be all the area an animal traverses during its lifetime.

The present data are interpreted to indicate that the mechanism of homing in *P. gossypinus* involves random movements outside the life range with respect to the homesite and directed movements in relation to the home area from within the life range. In the latter case the animal utilizes a previous familiarity (mnemonotaxis) with the general area gained by occasional exploratory wandering, home range shifting, and dispersal from the birthplace. Each of these movements apparently involves environmental imprinting.

INTRODUCTION

Homing ability and the general problem of spatial orientation have received increasing attention in recent years and have been investigated in widely diverse groups of animals. A considerable number of studies of small terrestrial mammals, principally rodents, have included information on the homing ability of the species con-

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cerned (*e.g.*, Aldous, 1937; Allen, 1938; Andersen, 1951; Bowers, 1954; Burt, 1940; Butsch, 1954; Feniuk and Demiashev, 1936; Feniuk and Popova, 1940; Feniuk and Sheikina, 1938; Hacker and Pearson, 1951; Hamilton, 1937, 1959; Harrison, 1958; Hungerford and Wilder, 1941; Johnson, 1926; Kalabukhov and Racoskii, 1933; Keith and Waring, 1956; Kendeigh, 1944; Layne, 1954, 1957; Linsdale, 1946; Löhr, 1938; McCabe, 1947; Murie and Murie, 1931, 1932; Rawson, 1956; Schleidt, 1951; Schmid, 1936; Seton, 1909; Stickel, 1949; Townsend, 1935). Data on homing have been obtained more or less incidentally to other aspects of the biology of the species being studied. Relatively few investigations, such as those of Rawson (1956), Schleidt (1951), and Stickel (1949), have dealt specifically with homing behavior of small mammals and have involved systematic field and laboratory procedures.

The information presently available on homing in small mammals clearly indicates that there is a general tendency among individuals of many species to return to their home areas when artificially displaced.

There are two major aspects involved in seeking to understand homing behavior in small mammals and other animals as well. The first of these concerns the nature of the motivation to return home. In other words, why should an animal placed in new surroundings similar to those in its home area exhibit a strong inclination to return to its previous quarters? This consideration leads to the question of what factors in the environment of a small mammal constitute "home" to that animal and what is the underlying psychological and physiological basis for the recognition of, and attachment for, the home area. Although much attention has been given to measurements of home range size in mammals, the problems of the psychological implications of the home range to the individual have thus far been largely neglected.

The second aspect involves the actual means utilized by an animal in its efforts to return to the home area. Various hypotheses concerning this problem have been suggested. Some workers such as Chitty (1937) and Layne (1957) have proposed that animals return from unfamiliar territory through random wandering until and if familiar surroundings are encountered, whereas others, including Burt (1940), Feniuk and Popova (1940), Feniuk and Sheikina (1938), Neuhaus (1948), and Vogelburg and Kruger (1951), have postulated the existence of some special sense of direction. The possibility that some animals actually possess a greater range of familiarity with the area around their homes than conventional study techniques indicate has also been suggested as a factor in homing success (Chitty, 1937; Kendeigh, 1944; Murie and Murie, 1931; Stickel, 1949, 1954).

The present paper concerns an investigation of homing behavior in the cotton mouse, *Peromyscus gossypinus* (LeConte), in north central Florida. The study, utilizing approximately 175 individual

cotton mice, involved: 1) establishment of home range and population estimates as necessary background for other phases; 2) displacements at various distances from the capture site to determine the extent of homing ability in natural areas; 3) homing releases in unfamiliar and unnatural habitat of animals from adjacent natural populations at distances similar to those used in natural areas for the purpose of comparing homing performance, 4) observations on initial orientation with respect to the homesite of animals released in unfamiliar and unnatural habitats, and 5) retention experiments involving the holding of animals in laboratory isolation for extended periods of time to learn the effects of such treatment on subsequent homing performance and home range recognition.

Acknowledgments.—I wish to express my appreciation to Dr. James N. Layne for his helpful criticism and numerous suggestions throughout the course of the investigation. Drs. Pierce Brodtkorb, Robert DeWitt, Lawrence Hetrick and James Redmond read the manuscript and helped in various ways. I am indebted to Mrs. Helen Phifer Glass for her generosity in permitting the use of her property at San Felasco for ecological studies. Dr. H. K. Wallace and Messrs. William H. Etheridge, Dale Birkenholz, Lee Frazer, Glenn Simpson and J. Hill Hamon assisted me during some phases of the study. Financial assistance was received from the Florida Academy of Sciences, and field work during the summer of 1957 was made possible by a fellowship from the College of Arts and Sciences, University of Florida. This paper is part of a doctoral dissertation submitted to the faculty of the graduate school of the University of Florida.

DESCRIPTION OF THE STUDY AREAS

The studies were conducted at four localities in Alachua County; these will be designated as San Felasco, Devil's Millhopper, Ft. Clark and the golf course.

The San Felasco area was located approximately 9 miles northwest of Gainesville. The general region consisted of an extensive mixed hardwood forest, with such trees as laurel oak (*Quercus laurifolia*), magnolia (*Magnolia grandiflora*), holly (*Ilex opaca*), sweet gum (*Liquidambar styraciflua*), and ironwood (*Ostrya virginiana*) being characteristic. This vegetative association, termed mesophytic hammock (Laessle, 1942), has been considered to represent the climax community of much of northern Florida (Figs. 1 and 2).

The Devil's Millhopper study site, located approximately 6 miles northwest of Gainesville, consisted of some 90 acres of mixed woodland with a network of trails and footpaths extending throughout the plot. The general aspect of the vegetation was similar to the San Felasco area except for some dry sections supporting grassy pine flatwoods. The Devil's Millhopper station was bordered on the south by a paved road and pine flatwoods and on the remaining sides by farmland.

The Ft. Clark area was situated about 8 miles west of Gainesville, and consisted of approximately 200 acres of mesophytic ham-



Fig. 1.—View of San Felasco study area.

mock that was somewhat drier than the San Felasco study site. The woodland was bisected by a sand road 50 to 65 feet in width. The area was generally flat and vegetatively relatively uniform throughout. It was bordered by farms, a limestone quarry, and the remnants of a cut-over pine flatwoods.

The golf course used in the study was located at the western edge of Gainesville. Its over-all dimensions were approximately 2200 by 2200 feet, and it was bordered on the north by a paved highway, on the east by a residential section, and on the south by cultivated lands of the University of Florida Agricultural Experiment Station. At the western edge of the golf course was a fringe of woodland bordered by a sand road. A hammock of approximately 40 to 45 acres in extent was situated on the other side of the road. The latter was 30 to 45 feet wide and was subject to frequent traffic during the morning and afternoon but little at night. The fairways of the golf course varied from 100 to 200 feet in width and were kept closely cut during the time the experiments were conducted (Fig. 3). The fairways were separated by park-like stands of oaks and pines. Although gray squirrels (*Sciurus carolinensis*) inhabited these stands, there was no evidence that cotton mice occurred there naturally.

HOME RANGE SIZE AND POPULATION DENSITY

In order to better interpret homing results, background information on the extent of normal movements of individual mice and on population densities in the habitat-types studied was obtained.

HOME RANGE

Data on home range were obtained at the San Felasco station. An area of approximately 20 acres was gridded with stakes at 100-foot intervals, giving a total of 88 trapping stations. Two types of live traps, the small (2 inches \times 2 1/2 inches \times 6 inches) Sherman trap and a plywood trap with inside dimensions of 2 1/2 inches \times 3 inches \times 8 inches, were used in this and other phases of the study. Rolled oats were used exclusively as bait. Trapping specifically for home range data was conducted for 11 nights during two periods, 6 nights from March 22 to March 28, and 5 nights from April 4 to April 9, 1959. Additional home range data for this population were accumulated incidental to other phases of the study until July, 1959.

All stations were trapped simultaneously with one trap per station. Mice were identified by a system of toe-clipping. Information recorded at each capture included date, trap station, sex and reproductive status, and escape path and refuge site used when liberated. Traps making captures were rebaited and reset at the same station but not in the same position as before.

Forty-eight cotton mice (25 males, 20 females, 3 juveniles) were trapped a total of 194 times during the course of the home range study. Four to ten captures were available for each of 25 adults (12 males, 13 females) taken a total of 145 times. Of the remaining 23 animals taken, 12 (1 adult male, 4 subadult males, 1 subadult female, 3 adult females, 3 juveniles) were captured only one time



Fig. 2.—General view of type of natural habitat in which studies were conducted.



Fig. 3.—View of one of the release points on the golf course.

each and 11 (4 subadult males, 4 adult males, 2 subadult females, 1 adult female) were taken two to three times each for a total of 26 captures.

Home ranges were calculated by the inclusive boundary strip method (Stickel, 1954) for the 12 adult males and 13 adult females taken a minimum of four times each.

The mean trap-revealed home range was $1.57 \pm .17$ acres. This value is comparable to that, $1.87 \pm .22$ acres, found by McCarley (1959) for *P. gossypinus* in Texas. The home ranges of 12 males averaged $1.82 \pm .36$ acres, with extremes of 0.45 and 4.36 acres, while those of 13 females averaged $1.44 \pm .19$ acres, with extremes of 0.22 and 2.75 acres. Although the difference in home range size between the sexes is not statistically significant, it suggests that males tend to have a larger home range than females. Other studies of this species indicate a similar trend.

Pournelle (1950) reported wandering of up to 2800 feet for a male cotton mouse while females appeared to move much shorter distances, and Pearson (1953) found that females of *P. gossypinus* generally moved less than 125 feet between release and recapture while males generally moved more than 125 feet. Barrington (1949) has shown that males of this species sometimes wander more than one mile while females wander about 800 feet between captures. Larger average home range size for males than females has been found for other species of *Peromyscus* (Burt, 1940; Blair, 1940, 1942) and similar data are available for a variety of other small mammals.

POPULATION DENSITIES

The number of mice estimated to be resident on the San Felasco study area was 36 (20 males, 16 females), which is equivalent to 1.6 animals per acre. Only mice with two or more captures were considered as residents, and the density is calculated on the basis of an adjusted sampling area which compensates for the probability of some animals having home ranges extending beyond peripheral traps (Dice, 1952). A rough estimate from live trapping results indicated that population densities were relatively the same at the four study sites.

HOMING IN NATURAL HABITATS

Mice used in homing experiments were removed from the traps in the morning and maintained in the laboratory until the time of liberation at night, thus eliminating at least some of the supposed effects, such as increased predation, of releasing nocturnal animals during the day. The mice were always conveyed to and from the study area and laboratory in numbered traps placed in a large container. The movements involved in transporting them over the study area and in the car are considered to have prevented the animals from utilizing kinesthetic cues in subsequent homing tests. Great care was taken to reset traps in the same place each time in an attempt to increase the probability of recapturing an animal upon its return.

Homing experiments were carried out at three natural study areas. Since the methods of study differed somewhat in each of these, the results of the experiments in each area are treated separately below.

SAN FELASCO

Following completion of home range studies, homing experiments were conducted on the trapping grid at this station. Individuals were displaced at relatively short distances beyond the limits of their known home ranges. A displacement of 300 feet was approximately equal to the diameter of the average home range. Animals were recorded as having successfully homed if they were recovered at any station within their calculated home range. Eighteen mice were trapped and displaced during an 18-day interval of irregular trapping. All trap stations were activated during each trapping period. Animals returning from their first release were often released in another direction and at a different distance. Thus, 5 mice were liberated one time, 6 mice were liberated two times, 1 mouse was liberated three times, 4 mice were liberated four times and 2 mice were released five times.

Initial releases were made as follows: 2 males and 1 female at 100 feet, 1 male and 1 female at 150 feet; 1 male and 2 females at 200 feet, 1 male and 1 female at 300 feet, 1 female at 400 feet, 2 females at 500 feet, 2 females at 600 feet, 1 male at 800 feet, and 1 male and 1 female at 900 feet.

Of the 7 males and 11 females displaced, all of the males and

10 of the females successfully homed. A male released at 300 feet was recovered on one occasion one-half the distance to its home range before it was recaptured in its home area. The female that was not recovered was an adult released at 600 feet.

Subsequent liberations of successfully homing animals included 19 releases of females as follows: 2 at 100 feet, 1 at 150 feet, 1 at 200 feet, 2 at 250 feet, 3 at 300 feet, 1 at 350 feet, 2 at 400 feet, 2 at 500 feet, 1 at 550 feet, 2 at 600 feet, 1 at 750 feet, and 1 at 800 feet. In a series of 9 males, 2 were released at 200 feet, 1 at 250 feet, 2 at 300 feet, 1 at 500 feet, 2 at 600 feet, and 1 at 700 feet. Recoveries were made in the case of all males and 18 of the 19 female releases. The female not retaken had been released a second time at a distance of 500 feet in the opposite direction from the first liberation at 600 feet.

The trapping schedule used at San Felasco was such that traps were not always available until several nights following releases. Therefore, it is not possible to present a detailed analysis of the times required for homing at this station.

It is of interest to note that although in many cases released mice had to travel through a portion of the grid of traps to reach

TABLE I.—Results of initial releases in the three natural habitats

Distance displaced	Animals displaced		Animals recovered	
	Males	Females	Males	Females
Feet				
100	2	1	2	1
150	1	1	1	1
200	1	2	1	2
300	1	1	1	1
400	..	1	..	1
500	4	6	4	6
600	..	2	..	1
800	1	1	1	1
900	2	1	2	1
950	1	1	1	1
1000	2	2	1	2
1050	3	..	2	..
1150	1	..	1	..
1500	2	2	2	1
2000	2	3	2	1
2100	..	1	..	1
2500	4	2	2	0
Totals	27	27	23	21

their respective home ranges, only one individual was taken in a trap beyond the boundaries of its previously calculated home region.

DEVIL'S MILLHOPPER

Homing experiments in this area were conducted using 30 trapping stations spaced 20 paces apart in an L-shaped trap line. Two traps were set at each station. Single displacements of 8 males and 9 females were made at distances ranging from 500 to 2000 feet from the place of capture. The releases were made during a trapping period of six consecutive nights in March, 1959, and traps were available for recapture on the night of liberation. Mice were considered to have successfully homed if they were retaken at the original site of capture or in either of the adjacent stations. The 17 displacements included in Table I were made as follows: 2 males and 2 females at 500 feet, 2 males and 2 females at 1000 feet, 2 males and 2 females at 1500 feet, and 2 males and 3 females at 2000 feet. Of these mice, 7 males and 6 females homed.

FT. CLARK

At this study area, homing tests were performed with 12 males and 7 females during April, May, and June, 1959. Two trapping periods were used, each of six consecutive nights. Ten trapping stations were established. Five were located on each side of the sand road about 50 feet within the woodland at intervals of approximately 100 feet. Three traps, spaced 10 to 15 feet apart, were used at each station. Release distances ranged from 400 to 2500 feet from the site of original capture, and mice were considered to have homed only if they returned to any of the three traps at the station of original capture. Successfully homing mice were liberated a number of times, usually at another distance and a different direction from that of their first release.

TABLE II.—Animals that were unsuccessful in homing from initial releases at Ft. Clark and Devil's Millhopper

Release distance	Sexes and numbers of animals		Number of consecutive nights traps were available following release
	Males	Females	
Feet			
1000	1	..	4
1050	1	..	5
1500	..	1	4
2000	..	2	5
2500	1	..	3
2500	..	1	4
2500	1	1	5

Ten mice were liberated 1 time, 2 mice were liberated two times, 4 mice were liberated three times, 2 mice were displaced four times, and 1 mouse was released five times. The numbers, sexes and distances involved in the initial releases of the 19 animals are included in Table I. Thus, 2 males and 2 females were released at 500 feet, 1 female at 800 feet, 1 male at 900 feet, 1 male and 1 female at 950 feet, 3 males at 1050 feet, 1 male at 1150 feet, 1 female at 2100 feet, 4 males and 2 females at 2500 feet.

Nine males and 5 females were recovered at the station where first captured, even though many of the displacements were made at a point that made it likely that the mice would encounter traps at several stations if they were to use the direct route in returning to their homesites.

Six of the 19 mice were displaced in the woodland on the opposite side of the road from which they were captured and 3 of these animals were recovered. Two of these individuals, a male and a female, had been displaced at 950 feet and the third, a male, had been released at 2500 feet. Those mice not retaken after removal to the opposite side of the road included 2 females liberated at 2500 feet and 1 male released at 1050 feet.

Of 20 subsequent releases, 9 of them were made in the woodland on the opposite side of the road from which they were captured. Five males released at 550, 850, 900, 1200 and 1450 feet, were retaken at their homesites and therefore had to traverse the sand road in returning. The 4 mice not retaken included a male and 3 females liberated at 1200, 500, 800, and 900 feet respectively. Apparently the road did not constitute a strong barrier to homing.

SUMMARY OF EXPERIMENTS IN NATURAL HABITAT

Of 54 mice (27 males, 27 females) displaced for the first time at distances ranging from 100 to 2500 feet, 44 animals (81%) were considered to have homed. Eighty-five per cent (23) of the males and 78 per cent (21) of the females returned. Every individual of both sexes homed from distances up to 500 feet. At distances from 600 to 2500 feet, 14 of 18 males (78%) and 9 of 15 females (60%) were retaken, indicating that males are more successful than females in homing from the greater distances (Tables I and II). A grand total of 101 releases (51 for males, 50 for females), including initial and repeated releases of homing animals, was made at distances varying from 100 to 2500 feet and homing was recorded for 83 per cent of the releases. Eighty-six per cent of male releases and 80 per cent of the female releases resulted in homing. Of the releases ranging from 100 to 500 feet, all of the males (17) and 92 per cent of the females (25 of 27) returned. Of the releases ranging from 550 to 2500 feet (34 male releases, 23 female releases) 79 per cent (27) of those of males and 65 per cent (15) of those of females returned home. At the Ft. Clark area 4 of 19 (21%) mice used in initial releases and 10 of 20 (50%) used in subsequent releases were recap-

TABLE III.—Results of subsequent releases of animals that successfully homed from initial releases at Ft. Clark

First release			Subsequent releases	
Sex	Distance in feet	Recapture interval*	Distance in feet	Recapture interval*
M	500 W	1	450 NE 1200 E	1 No recapture (3)**
F	500 E	2	400 N 900 SE	1 No recapture (3)**
M	500 W	2	450 NE 1200 SE	1 3
F	500 W	2	1150 E 2000 E	(3) (7) (46)*** 2
F	800 W	3	800 E	No recapture (2)**
M	900 E	2	1450 SE 2000 E 2500 E	1 1 No recapture (2)**
F	950 NW	1	500 N	No recapture (4)**
M	950 N	2	850 E 900 NE 700 W	1 1 1
M	1050 E	3
M	1050 E	5
M	1050 E	1	550 SW 850 NE 1200 N 1850 E	(1) (2) (41)*** 1 1 No recapture (3)**
F	2100 E	1
M	2500 E	2
M	2500 E	3

* Night of release is designated as night 1.

** Figure in parenthesis indicates the number of consecutive nights traps were available immediately following release (uninterrupted).

*** First figure in parenthesis represents the number of consecutive nights that traps were available immediately following release (uninterrupted); second figure represents actual trap night the animal was recovered; third figure in parenthesis indicates the total nights elapsed between release and recapture.

tured on the night of liberation (Table III). This suggests, therefore, that homing performance of animals liberated away from home subsequent to the first successful homing trip tends to improve, even though the distances and directions of successive releases are varied.

The results of the homing experiments in natural habitats indicate that homing success in the cotton mouse is inversely proportional to distance at which released. There is a further indication that males and females home with equal success at shorter distances (<500 feet), while males have a greater probability of homing than females as release distances are increased. The data further suggest, although the relationship is not clear-cut, that, for the range of distances utilized, homing from the initial release is more rapid at the shorter distances (Table IV). Homing success also appears to improve at both short and long distances with repetitive liberations, even though these are not made at previous release points (Table III).

Similar results have been obtained in other studies. For example, Murie and Murie (1931) recorded 87.4 per cent return from displacements up to 900 feet and only 30.6 per cent from 1050 to 3900 feet for *P. maniculatus*, if only those animals released away from home

TABLE IV.—Release/recapture intervals of initial releases at the Devil's Millhopper and Ft. Clark study sites

Release distance in feet	Animals recaptured in their home areas		Recapture interval in nights*
	Males	Females	
500	2	2	1
500	2	2	2
800	..	1	3
900	1	..	2
950	..	1	1
950	1	..	2
1000	1	1	1
1000	1	1	3
1050	1	..	3
1050	1	..	4
1150	1	..	1
1500	1	..	2
1500	1	1	3
2000	1	..	2
2000	1	..	3
2000	..	1	5
2100	..	1	1
2500	1	..	2
2500	1	..	3

* Night of release is designated as night 1.

for the first time are considered. Harrison (1956) working with *Rattus*, reported 83 per cent recovery from 1650 feet and 38 per cent recovery from rats liberated at 2640 feet. Hacker and Pearson (1951) have noted a similar trend in homing ability in *Apodemus sylvaticus*, and Burt (1940) in a study of *P. leucopus*, showed that 76 per cent of the mice were retaken from displacements of 30 to 465 feet while only 33.3 per cent of those liberated from 480 to 1095 feet were recovered.

HOMING FROM UNNATURAL HABITAT

From March to early September, 1959, homing studies were carried on at the golf course, utilizing mice from adjacent natural habitats. The object of this phase of the study was to obtain data on homing success from what could be considered totally unfamiliar and unnatural habitat for comparison with those obtained in natural habitats. Trapping was conducted in two wooded plots located in the northwest and southwest corners of the golf course and in the hammock west of the sand road. Sixteen trapping stations were established in the northwest corner where the habitat suitable for cotton mice was limited to approximately one-half acre. At the southwest corner 12 trapping stations were used, the area being somewhat smaller than that in the northwest corner. The same stations were used throughout the study. No particular arrangement or spacing of traps was utilized, and mice were considered to have successfully homed if retaken at any of the traps in which they were originally captured, since the areas were small enough to correspond with the home range of the animals. In the large woodland, 40 stations were arranged in a U-shaped pattern with about 30 yards between stations. Mice were recorded as successfully homing if retaken at the original site of capture or in either of the adjacent trapping stations. Single traps were used at the stations in the study plots at the edge of the golf course and two traps set within 10 to 20 feet of each other were used in the hammock west of the road.

Animals captured in the peripheral areas were released at selected sites on the fairways. No release site had trees nearer than 100 feet. Some of the successfully homing animals were released a number of times from the same release point to learn the effect of repetitive liberations in unnatural habitats on homing performance. In a very few instances, the release site was shifted between successive releases.

Forty-seven mice were initially released on the golf course at distances ranging from 1000 to 2700 feet from the site of capture in the adjacent woodlands. In all cases, traps were available for recapture for three nights, including the night of release, and in many instances for as long as 7 to 21 nights after each series of releases. Three males, 2 females, and 1 juvenile were released at 1000 feet, 1 male and 1 female at 1700 feet, 1 male and 2 females at 1800 feet, 4 males and 1 female at 1900 feet, 3 males and 3 females at 2200

feet, and 18 males and 7 females at 2700 feet. Fifteen of these animals (10 males, 5 females) were subsequently recovered at their homesites. All of the animals that returned from 1900 feet or more had to cross the sand road in order to reach their home areas.

One male that homed from 2700 feet was not recovered during the four consecutive nights that traps were available following displacement, but was recaptured on the third night after liberation at a point 2500 feet north of its original capture site. This individual was later recovered in its home area on the first night of a trapping period, 40 nights after the original displacement. Traps had been available to this animal a total of 14 nights between the time of liberation and subsequent recapture in its home area.

Several animals were recaptured at places other than their home areas. Two males and a female at 2700 feet and a male released at 2200 feet northeast of their respective homesites were trapped approximately 2500 feet north of the homesite. The single juvenile released 1000 feet west of its home area was recaptured 2200 feet south of the site of original capture, and a female displaced 2200 feet northeast of its homesite was recovered 400 feet east of the original capture site.

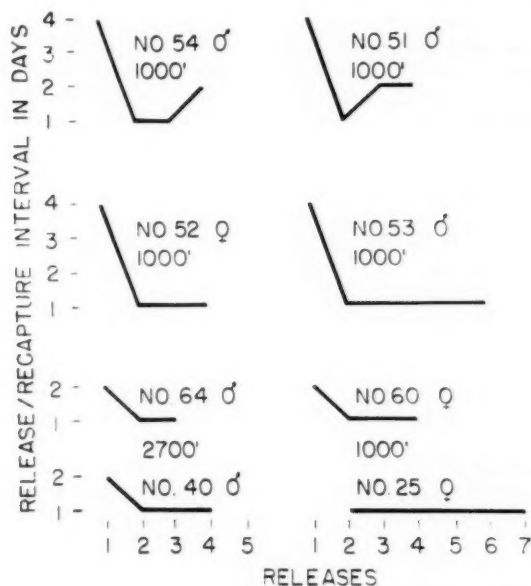


Fig. 4.—Effect of multiple releases from the same point on time of return in golf course experiments.

Seven of the 15 animals recaptured in the home area were liberated a number of times from the same release point. The results of these tests clearly indicate that the animals home more rapidly from the same release site following the first return. This trend is illustrated in Fig. 4, where the length of time taken by the mice to return from successive releases from the same point over distances of 1000 to 2700 feet is shown graphically. In most instances time intervals were measured in nights, since traps were checked only on the morning following release. However, on one occasion periodic checks were made after release and a close approximation to the actual time taken to return from 1000 feet was obtained for 3 animals that had homed from the same point previously. A female, No. 60, released for the third time, returned in less than three hours. Another female, No. 52, and a male, No. 53, which had been released for the third and fifth times, respectively, were back in the traps within two hours.

These results are summarized in Table V. Of 6 mice (3 males, 2 females, 1 juvenile) released at 1000 feet, only the juvenile did not return to its homesite. Ten mice (6 males, 4 females) were liberated at 1700 to 1900 feet and 3 males and 2 females were recaptured. Four males and 1 female, of 31 animals (21 males, 10 females) liberated at 2700 feet, were recovered. No recaptures were recorded on the night of release. Six of the 15 animals that homed returned by the second night following liberation; the other 9 mice took an excessive amount of time for recovery (Tables VI and VII). Of the total number of adult mice released (46) on the golf course at 1000 to 2700 feet, 5 of 16 females (31%) and 10 of 30 males (33%) returned to their home areas. Successfully homing animals released repetitively from the same point at distances ranging from 1000 to 2700 feet from the homesite clearly improved their homing performance.

TABLE V.—Results of initial releases in unnatural habitat (golf course)

Distance displaced	Animals displaced		Animals recovered	
	Males	Females	Males	Females
Feet				
1000*	3	2	3	2
1700	1	1	1	1
1800	1	2	1	1
1900	4	1	1	0
2200	3	3	0	0
2700	18	7	4	1
Totals	30	16	10	5

* One juvenile was displaced 1000 feet but was never retaken at its home area.

The data from homing releases made on the golf course provide a basis for comparison with those in natural areas. It should be pointed out that the highway, residential areas, and cultivated lands at the northern, eastern, and southern borders of the golf course could have acted as barriers to the animals and may have directed their movements to some extent. The sand road bordering the west side of the golf course may to some extent have been a barrier to homing but the recovery of some individuals from the mesophytic woodland on the other side of the road indicates that it probably did not hamper movements excessively. The results of the Ft. Clark experiment further support this contention.

The shortest distance at which releases were made on the golf course was 1000 feet. The homing success at this distance was closely similar to that in natural habitats. However, nearly all animals released at this distance in natural habitats were recovered by the second night following liberation. In the case of the golf course releases only 1 animal returned by the second night of trapping. Other animals released at 1000 feet took more than four nights to return.

Three of the 10 mice liberated at 1700 to 1900 feet on the golf

TABLE VI.—Release/recapture intervals of initial releases on the golf course

Release distance in feet	Animals Recaptured at their home areas		Recapture interval in trap nights*		
	Males	Females			
1000	..	1		2	
1000**	3	..	(4)	(5)	(35)
1000**	..	1	(4)	(5)	(37)
1700	1	1		2	
1800	1	..	(7)	(11)	(17)
1800	..	1		2	
1900	1	..		4	
2700	2	..		2	
2700**	1	..	(6)	(7)	(26)
2700**	1	..	(4)	(14)	(40)
2700**	..	1	(6)	(13)	(40)

* Night of release is designated as night 1.

** Figures in parentheses represent the following: First figure — the number of consecutive nights that traps were available for recapture immediately following release though the animal was not recovered during this time; Second figure — the actual trap night that the animal was retaken; Third figure — indicates the interval of time between release and eventual recapture.

course returned by the second night following release. All of these mice were residents of the southwest corner of the golf course which was near rows of pig pens on the Agricultural Experiment Station lands. The loud and frequent clanging of the feeding trough doors by the pigs may have provided an auditory cue for these mice which might explain their relatively rapid return. Two other mice homing from 1800 and 1900 feet took an excessive amount of time to be recaptured. Four of the 6 mice released at 2000 and 2100 feet in natural areas were retaken, 1 on the night of liberation, 1 on the second night, 1 on the third night, and 1 on the fifth night of trapping. In comparing homing success in natural habitat to homing success from the golf course, no clear-cut difference was found at release distances ranging from 1700 to 2100 feet although there is a tendency for mice to return more rapidly in natural areas.

Of the 31 animals released at 2200 feet or more on the golf course, only 2 were recaptured by the second night following release. Three other mice released at this distance took considerably longer, and as noted 1 of these was retaken 2500 feet north of its home-site before it was recaptured in its home area. In natural areas 2 of 6 mice released at 2500 feet were recaptured, 1 by the second and the other by the third night following liberation. Both of these were males. Considering that traps were available for recapture in

TABLE VII.—Animals that were unsuccessful in homing from initial releases on the golf course

Distance released	Males	Females	Number of nights that traps were available for recapture following release	
			Consecutive nights beginning with the night of release	Total nights
1000	Juvenile		7	14
1800	..	1	7	11
1900	1	..	7	18
1900	1	1	8	19
1900	1	..	10	21
2200	..	1	5	16
2200	2	..	7	11
2200	1	2	8	16
2700	5	1	3	3
2700	..	1	3	11
2700	..	1	4	12
2700	2	..	4	7
2700	5	3	6	14
2700	2	..	4	12

the peripheral areas of the golf course for a much longer period of time than in natural areas and that the nature of the area surrounding the golf course might have to some extent directed the movements of the animals westward, which was in the direction of the home area, the results strongly suggest that mice home with greater success in natural areas.

INITIAL ORIENTATION

From February to early September, 1959, observations were made on the initial movements of animals liberated at night on the golf course. Two groups of mice were used, a "local" series (also used for homing experiments) captured less than one mile from the release site and a "distant" series captured from four to 60 miles from the release area. The mice used in these experiments were captured in the morning and kept for 12 to 15 hours in the laboratory until the time of liberation at night. Several mice from the local sample were held in captivity up to 65 hours before release because of inclement weather, and 4 mice from 60 miles away were kept in the laboratory 13 days before release.

A step-ladder painted black for camouflage was used at the release site as an observation point. The experimental animal was transferred from a live trap to a bottomless hardware cloth cage measuring 5 inches \times 3 inches \times 3 inches and placed on the ground beneath the center of the ladder. After the mouse had been allowed a period of time for adjustment to its surroundings, the observer, seated on top of the ladder, gently raised the cage by means of an attached string.

A strip of cellophane tape with a 1 1/2 inch patch of luminous paint ("Lite Koat Mixture" manufactured by the General Cement Company, Rockford, Illinois) previously charged by a flashlight in a light-tight box was affixed to the dorsum of the mouse just before it was transferred to the release cage. After liberation the mouse was observed directly or with the aid of a pair of 7 \times 50 binoculars. The pattern of its movements was traced in as great detail as possible on data sheets which also included the date, time of night, location of homesite, temperature, wind direction and velocity, sky conditions, and other details. The animals were marked for permanent identification by toe-clipping.

The maximum distance any mouse was observed from the release point was approximately 175 feet and many of the mice required 12 to 13 minutes to move beyond the observer's range of vision.

Overcast or moonless nights provided best conditions for observations. The luminescent patch remained visible for approximately 15 minutes. The initial movements of mice in both groups were characteristically slow and usually very erratic. Randomly selected examples of initial movements from the two groups are shown in Figures 5 and 6. In some instances the animals moved in spurts and occasion-

ally followed a more or less circular pattern, sometimes returning to the release point several times. No correlation between speed of departure or the animal's initial course and the proximity or direction of the homesite was apparent under a variety of environmental conditions, including overcast and clear nights with and without a moon. However, clear moonlit nights tended to inhibit movements of the mice, which seemed hesitant to leave the area of shadow created by the observation post.

Further evidence that initial orientation movements on the first release were random with respect to the homesite is provided by an analysis of the selection of particular directional zones by mice when released. An imaginary line was drawn from the release point to the approximate homesite. Using the home bearing at the base line, the release area was divided into four equal zones. Zone +I included the sector encompassed by a 45 degree angle on either side of the

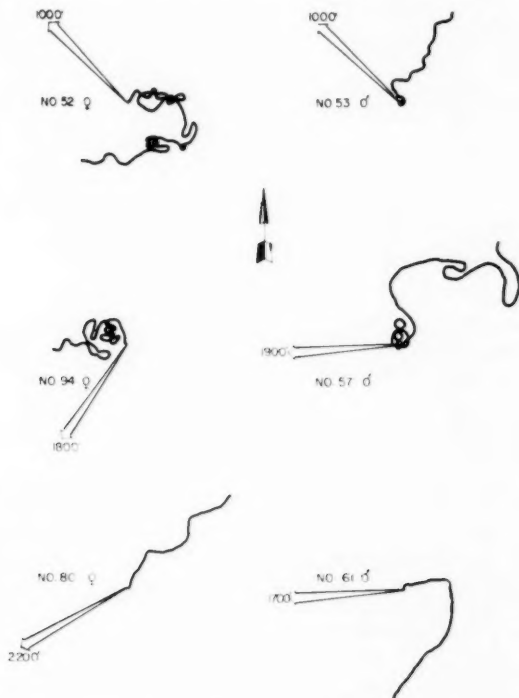


Fig. 5.—Initial orientation patterns in unfamiliar territory of mice from the "local" population. The direct homing route for each animal is indicated by the arrow originating at the release point.

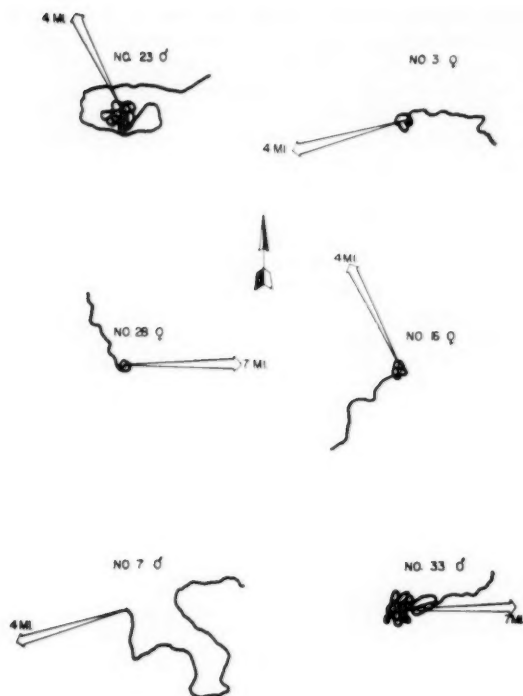


Fig. 6.—Initial orientation patterns in unfamiliar territory of mice from the "distant" populations. The direct homing route for each animal is indicated by the arrow originating at the release point.

home bearing. Zone -I included the opposite 90 degree sector, and the lateral zones were designated as 0_1 and 0_2 .

Of 47 mice comprising the local sample, 10 (6 males, 4 females) selected Zone +I, 11 (8 males, 2 females, 1 juvenile) Zone 0_1 , 12 (8 males, 4 females) Zone 0_2 , and 14 (8 males, 6 females) Zone -I. In the case of the 42 mice constituting the distant sample, 9 (6 males, 3 females) selected Zone +I, 11 (7 males, 4 females) Zone 0_1 , 8 (4 males, 4 females) Zone 0_2 , and 14 (6 males, 8 females) Zone -I. The difference in these frequencies are not significant in either series on the basis of the chi-square test (local sample $X^2 = 0.95$, distant sample $X^2 = 1.98$).

The 15 animals from the local population that were subsequently recovered at their homesites had selected the following zones on their first release: Zone +I, 1 male released at 1800 feet and a female released at 1700 feet; Zone 0_1 , 1 male released at 1000 feet, 1 fe-

male released at 1800 feet and a male and female released at 2700 feet; Zone 0₂, a male released at 1700 feet, 3 males released at 2700 feet and 2 females released at 1000 feet; and Zone -I, a male released at 1900 feet and 2 males released at 1000 feet. There is no significant difference in the frequency of use of the four zones by these animals, indicating that even in the case of successfully homing mice there was no tendency to select the direction of the homesite when released for the first time in unfamiliar territory.

Seven of the 15 animals were regularly liberated and recaptured a number of times from the same release point. The observed movements at later releases were strikingly different from those of the first. In almost every test, the mouse moved rapidly and with little hesitation, often passing beyond observation range within 30 seconds. During the course of these repetitive releases, it was noted that some

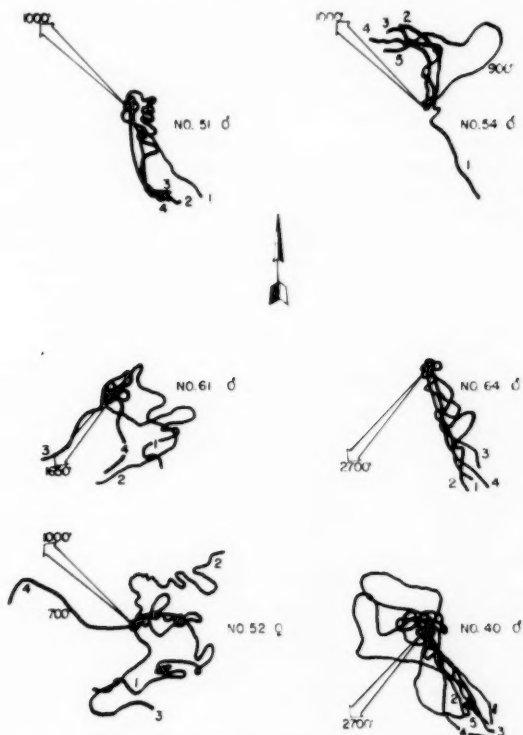


Fig. 7.—Initial orientation of 6 mice released repetitively at the same point on the golf course. The direct homing route for each animal is indicated by the arrow originating at the release point.

mice appeared to utilize the same initial pattern of movement as on the first release, even though the pathway was unoriented with respect to the home direction. Such a tendency is indicated by mouse No. 51 whose initial orientation patterns are shown in Figure 7. One animal, male No. 54, on its fifth release at a point 100 feet closer to the homesite than the usual distance (1000 feet) exhibited a pattern of movements similar to that of previous releases (Fig. 7). Another individual, female No. 52, was liberated 300 feet closer to the homesite on the fourth release than previously. Its path was oriented in the direction of the home area. It is possible that on this occasion the animal may have been responding to heavy shadows of the wooded section, which was much closer than usual due to the decreased release distance (Fig. 7).

Of the other successfully homing animals from this group, 3 were not again used in this or other experiments. Five were subsequently released a total of 15 times at different points on the golf course varying from approximately 1000 to 2200 feet from their capture sites, and in general their initial movements were more rapid than on the first release. One animal was not recovered after its second release. The remaining 4 returned to their homesites in from one to three nights on several later occasions, which suggests that they may have acquired a familiarity with a considerable portion of the golf course as a result of previous releases.

Eleven of the 42 mice (26%) from "distant" populations were recovered at the peripheral areas of the golf course in the interval of

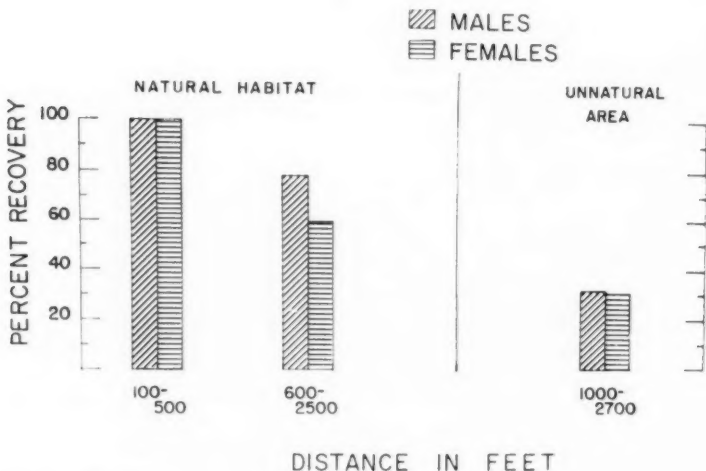


Fig. 8.—Comparative homing success of males and females in natural and unnatural habitats.

about four months after the initial liberation. Six of the 11 were released a second time at points different from the original ones. The distances ranged from approximately 1000 to 2000 feet from the last capture site. In general, these animals moved rather rapidly upon liberation though none of them was recovered again. The other 5 mice were released a second time at the original points, and their movements were also noticeably more direct. Four of these were recaptured again and released at other points on the golf course. In all, these mice were retaken on 17 occasions at different places and at intervals ranging from two days to four months between release and recapture. This suggests that the animals were wandering and had not established definite home ranges. The fifth animal was liberated a total of seven times at the same release point. Although its pattern of initial movements seemed to change with each release, this mouse, female No. 25, from a "distant" population (60 miles) consistently returned to the same trap in the northwest corner of the golf course on the same night that it was liberated (Fig. 4). On its third release at 1000 feet the animal was retaken in the usual trap within three hours after liberation. This suggests that some cotton mice that do not locate their former home ranges may settle quickly in a new area. Burt (1940), Murie and Murie (1931), and Stickel (1949) have noted a similar tendency for certain mice to remain in the vicinity of the release site.

Briefly stated, the results of the initial orientation experiments suggest that mice released in completely strange territory, whether near or distant from the home area, move in a random fashion from the release point with respect to the homesite. Animals that are successful in finding their home area and are released again at the original point may return by the previous pathway, although indirect. Their movements in subsequent trials, however, are more rapid because they are now traveling over familiar territory. Mice from distant sources that establish home ranges in the new region behave as do local animals on subsequent releases.

It is difficult to say exactly what cues the animals use for orientation under these circumstances. Vision probably plays an important role, although other sense modalities may also be involved to a significant degree.

RETENTION EXPERIMENTS

During the summer of 1959 several experiments designed to provide some indication of the degree of attachment for the home area and the role of learning and memory in homing behavior were conducted. Mice of varying previous homing experience were removed from the San Felasco and Ft. Clark study populations and retained in the laboratory for periods of time ranging from 32 to 87 days. During the period of retention the mice were kept in a small animal room which housed several other species of mammals. The mice were kept in small cages with two individuals of the same

sex per cage. Food and water were provided ad libitum and nesting material was supplied. After the retention period, the animals were returned to the study areas where they were liberated just prior to sundown. Some were released at different distances from the home area, while others were replaced within their former home ranges. Trapping was conducted for various periods of time afterwards to obtain data on the subsequent movements of the released animals.

The first experiment involved 12 animals (7 males, 5 females). Eight of these had been used in homing experiments at San Felasco and, therefore, were presumed to be familiar with some of the area immediately outside their trap-revealed home ranges. After laboratory isolation of from 34 to 35 days, a control group of 6 mice (2 males, 4 females) was liberated within the former home ranges of the individuals. Three females in this group had been used in homing experiments previously. Of the remaining 6 animals (5 males, 1 female) 5 were released at points that the individuals had presumably traversed in the original homing experiments. These releases included 1 male at 450 feet, 1 male and 1 female at 500 feet, and 2 males at 900 feet. A male in this group that had not been used in the original homing experiments was released at 700 feet. The distances given in each case were measured from the limits of the known home ranges to the release point. Traps were set on the grid prior to release and the area was trapped for five consecutive nights. Of the animals liberated in their former home ranges all were retrapped, the 6 mice being retaken a total of 12 times during the first trapping period. None of these individuals was taken in traps beyond the boundaries of the previously calculated home range. Only one animal was taken the first night of trapping. Five of the 6 mice liberated outside their former home ranges at distances ranging from 450 to 900 feet were retaken 11 times during the trapping period. One was retaken on the night of liberation 300 feet outside its home range but when retrapped the next night was within its former home area. All of the others were taken only within the calculated boundaries of their home ranges. The one animal not recaptured was a female liberated at 500 feet; it had successfully homed from the same distance in the original homing experiments.

Trapping in the area about six weeks later revealed that 7 of the 11 mice that were used in the retention experiment (the other 4 of the original group had been removed to the laboratory for another experiment) had remained in their original home ranges. These 7 animals were retaken 18 times during six nights of trapping, the recaptures of each being restricted to the previously calculated home range.

A second experiment was performed using 14 animals (7 males, 7 females) that were held in captivity for 32 to 34 days. One male was released within its former home range. The other animals were released outside their former home ranges as follows: 1 male and 2 females at 300 feet, 1 female and 2 males at 400 feet; 1 male at

500 feet, 1 female at 550 feet, 1 male at 650 feet, 1 male and 2 females at 700 feet, and 1 female at 900 feet. Four of the animals tested had been used in the previous experiment and therefore had been retained in the laboratory for more than 60 days with an interruption of five nights during the first experiment. Of the remaining 10 animals, 8 had never been used in any other phase of the study. Trapping was conducted for six consecutive nights beginning with the second night following liberation.

Thirteen of the 14 animals released were retrapped a total of 40 times. On the first night that traps were available, 2 mice were retaken outside their home ranges, although both animals were later (second and fourth nights) recovered in their respective home areas. All other mice were never recaptured outside of their original home ranges. Only 1 animal, a male liberated at 500 feet, was not retaken. This animal had not been used in any of the previous experiments and had a home range at the periphery of the study area which might have extended beyond the plot. Consequently, it probably had a lower probability of capture and might have returned without being recovered.

In some cases, observations were made on the initial movements of the animals at the time of liberation. On one occasion, 2 mice were released simultaneously at the same site. One of the individuals was known to have previously nested in a particular log about 10 feet from the release point, while the other mouse was 500 feet outside its former home range. The activities of the 2 mice were distinctly different, the one formerly occupying the area moved rapidly to a small hole in the log after a few seconds of hesitation, while the other mouse moved more slowly, lingering within a few feet of the observer and appeared to be examining various objects. The latter mouse was observed for about 10 minutes and was eventually lost in some fallen trees 30 feet from the release point and in the general direction of its former home area.

One mouse released in its former home range moved with little hesitation and on a direct course to a tree root 35 to 40 feet away that had been occupied during the home range studies some 15 to 16 weeks before. Another mouse released in its former home range moved a short distance away from me then turned and ran rapidly between my legs to a slight depression in the ground five feet from where it was liberated. The depression was completely covered with ground litter and did not appear to be a regular homesite. Closer examination revealed a small hole in a log buried beneath the litter. The mouse had apparently entered this hole, and its actions left the distinct impression that it had intentionally sought this refuge. The other animals liberated in this experiment were out of sight soon after release, and observations on their movements could not be made accurately.

Two more retention experiments were performed with 3 animals at Ft. Clark. The periods of isolation were 38 and 87 days. The

trapping plan, as already indicated, consisted of ten stations on either side of a sand road. Two males were used in the first experiment, 1 of the 2 having first been conditioned to homing from 950 feet and the other from 1200 feet. After 38 days of laboratory isolation, the individual conditioned to 950 feet was released at 700 feet. It was not recovered during subsequent trapping. The other male was liberated at 500 feet at a point making it necessary for it to encounter several trapping stations if it were to use the first direct route in returning home. This animal was recovered at its original homesite on the second night following release. After its first return, liberations were made at 1000, 1500, 2000, and 2500 feet. Several of these releases were in a direction that made it necessary for the mouse to encounter four trapping stations if it were to use the direct route in returning. In each case the animal was recovered at its homesite on the same night it was liberated.

This successfully homing male was again removed to the laboratory and isolated for an additional 87 days. A female conditioned to homing from 1150 feet was also retained for the same length of time. After the isolation period, both animals were released at 1000 feet on the opposite side of the road from which they were originally taken, making it necessary for the mice to cross the road if they were to regain their homesites. On the second night of trapping, both mice were recovered at the exact station where they had been caught previous to the period of isolation. Liberations at 1500 feet were then made, and both mice were back the same night. Further releases were not made, but during two nights of additional trapping, the male was retaken twice and the female once, indicating that they were persisting at their respective homesites. It is of interest to note that during the 87-day period the mice were kept in captivity the vegetational aspect of the study plot had changed markedly. A 5 to 10 foot wide strip of vegetation bordering the road had grown to approximately 5 to 6 feet from an initial height of about 1 foot, and the foliage had grown considerably denser.

The retention experiments seem to clearly indicate that the cotton mouse is able to recognize its former home range and retains a strong motivation to return to it even after a rather prolonged absence. The mice also appear capable of remembering for an equally long period of time terrain infrequently traversed and outside the normal limits of the home range.

DISCUSSION

Homing results obtained in the present study suggest, as do those for other small mammals, that cotton mice have a strong attachment to their current home range and are strongly motivated to return to this area when removed from it. The apparent lack of response to available traps outside the calculated home range observed in many instances may also be taken to indicate that a mouse responds differently to objects in the environment inside and out-

side of the familiar zone, which argues further that the familiar zone has a unique significance for the individual. Data from the retention experiments suggest that the memory of the home range and motivation to return to it are remarkably persistent when considered in relation to the average ecological longevity of six months reported by McCarley (1959) for the species in Texas.

The foregoing considerations appear to have implications in connection with our present concept of the home range of small mammals. Most attention given to the significance of the home range has emphasized the somatic aspects. That is, the home range is the area over which an animal travels in obtaining food, homesites, mates, etc., and with which it is intimately familiar and thus better able to find cover when escaping from enemies. It may be assumed that the home range not only satisfies the animal's physical needs, which might often be provided for equally well or better in other areas, but has some psychic significance. In other words, the home range offers a wide variety of associations with environmental objects to which the animal is intimately attached. Within this familiar area, the animal moves with assurance. If displaced artificially from its home area the animal may become psychologically disturbed. This state may also be accompanied by physiological changes similar to those symptomatic of stress, resulting in a search for familiar territory.

Although field-data to support this hypothesis are apparently nonexistent, laboratory experiments performed by Southwick (1959) have a bearing on the question. His results indicate that the mere transferring of adult animals to a new, but physically similar environment constitutes a relatively stressful experience. It is possible that under natural conditions wild rodents removed from the home area may show a similar response, even though the habitat in which they are released is physically similar to that of the home area. The accompanying psychological unrest may then stimulate them to look for their home areas.

Granted that small mammals have a "home sense" and are strongly motivated to return to their established home area, the question of the means by which this is accomplished must be considered. Celestial cues, including polarization patterns in the sky, the sun, stars, and moon, have been implicated in the orientation of several rather widely separated and diversified groups of animals (Carthy, 1956; Sauer, 1958). No evidence obtained in this study indicated that celestial bodies were used directly by mice in homing from the distances used, although such factors as shadows created by moonlight influenced to a certain extent the patterns and rates of at least initial movements after release. Rawson (1956) has indicated that mice successfully home under overcast skies from relatively short distances, and Bovet (personal communication), on the basis of preliminary experiments, has tentatively concluded that red mice

(*Evotomys* = *Clethrionomys*) and wood mice (*Apodemus*) do not utilize the sun in homing.

On the basis of the evidence gathered in this investigation, it is postulated that homing was accomplished in two ways: 1) random wandering in unfamiliar terrain until and if a familiar area was encountered, and 2) nonrandom movements in terrain with which the animal had some previous familiarity.

The first explanation appears to apply to the golf course experiments in which initial orientation of mice released for the first time was apparently random. In addition, the time required for recapture in homing tests was appreciably higher than in natural areas, and the proportion of recaptures from the greater distances was lower. The idea of random wandering is further supported by the observations on 4 mice whose recaptures during the several days following release suggested that the animals were unoriented with respect to a direct homing route. Animals which by chance select a pathway in the direction of their homesites may return in a short interval over a relatively long distance. Such returns may be aided by a directing influence of certain environmental features such as roads, waterways, open fields, and topographic irregularities.

Much of the homing recorded in this study is believed to have been a nonrandom activity with respect to the homesite. In other words, the animals had in actuality not been released in completely unfamiliar terrain. This view supposes that the mice are familiar to a certain extent with an area considerably larger than the calculated home range. There are several ways in which this broader knowledge of the environment may be gained. These include actually larger home ranges than are revealed by conventional methods, occasional exploratory sallies outside the home range, shifting of home ranges, and dispersal from the birthplace.

Chitty (1937) and others have suggested that small rodents may have larger home ranges than can be determined by standard trapping techniques. Such procedures as are presently employed in studying small mammal home ranges may merely give an index of the area an animal regularly encompasses in seeking its requirements. The various techniques of home range determination and the relationship between "trap-revealed" and "true" home ranges have been considered by Hayne (1949, 1950) and Stickel (1954).

Occasional trips beyond the usual home range would permit "exploratory learning" (Thorpe, 1956) and actually represent instances of "natural" homing. Such movements have been recognized in various small mammals (*e.g.*, Blair, 1940, 1943; Storer, Evans, and Palmer, 1944). Small mammals are also known to shift the home range from one period to another or expand or contract its limits (*e.g.*, Burt, 1940; Blair, 1940) and in this manner probably become familiar with additional terrain.

Dispersal from the birthplace may be a rather important way in which rodents obtain a knowledge of a larger general area than

ordinarily encompassed by the home range. In this connection, an analysis of dispersal and homing data obtained for *Peromyscus leucopus* and *P. maniculatus* by Burt (1940), Howard (1949), Stickel (1949), Dice and Howard (1951), and Murie and Murie (1931, 1932) supports the conclusion that at least part of homing success of small mammals can be attributed to familiarity with terrain acquired during dispersal. The tendency for recapture of fewer animals liberated at greater distances in homing experiments therefore seems to be related, among other things, to the dispersal of the species. The work of Levine (1960) appears to be especially significant to dispersal and homing behavior of small mammals. Levine has conclusively shown that manipulation and exposure to stresses during infancy enhances the development of normal stress responses in the adult animal. It seems likely that during dispersal from the birthplace immature mice would undergo a period of stressful experiences. Those animals dispersing the greater distances would not only learn more terrain but also would be better conditioned to a stress such as might be encountered in homing displacements. Thus, the greater the distance an animal is released from the homesite the less the chance it has had previous experience with the terrain and the lower its probability of return.

Records such as the one reported by Murie and Murie (1931) in which 1 of 23 animals released at two miles was recovered at its homesite in only 48 hours after liberation suggest that the animal may have had prior knowledge of the area gained, perhaps, during dispersal. Schleidt (1951) recovered 2 mice in about 10 to 15 minutes after releasing them at 1000 feet.

Much evidence points to the fact that in small mammals, males have a wider range of activity than females. In considering the sex differences in dispersal, the data of Burt (1940), Howard (1949), Dice and Howard (1951) and the paper of Howard (1960) appear to be significant. In general, their data show that short distance dispersal from the birthplace occurs with approximately equal frequency in males and females. Dispersal to the greater distances is, however, more frequent in males, often more than twice the percentage of females. The homing success of males and females of *P. leucopus* (Burt, 1940, and personal communication; Stickel, 1949) exhibits a close correlation with dispersal distance for that species. A sex difference in home range size with males averaging larger home ranges than females is indicated in this study and a similar trend has been reported for other species of small mammals. Barrington (1949), Pournelle (1950), and Pearson (1953) each reported a more extensive wandering habit in males of *P. gossypinus*. This evidence further suggests that males tend to be familiar with a greater area than females. If the suggestion that much of homing success in small mammals is the result of familiarity with the terrain surrounding the home area is correct, then one would expect to obtain higher homing success in males than females at least at the

greater distances. On the basis of this hypothesis, no difference in homing success of males and females released in totally unfamiliar territory would be expected. Such does appear to be the case in the golf course experiments where nearly the same proportion of males and females, 33 and 31 per cent, respectively, returned from first releases (Fig. 8). These results seem to indicate random wandering in unfamiliar territory.

The question now arises, are animals capable of learning the features of the terrain and homing pathways at an early age, and if they can, whether or not they can retain a memory of such familiarity for a prolonged period of time? Feniuk and Popova (1940), in their homing experiments with rodents, concluded that young mice (juveniles) that have not become independent of their nests do not show homing ability. The explanation of this may be two-fold. First they may lack the motivation needed for homing and second they may lack the familiarity with the terrain around their birthplaces.

This suggests that the dispersal and establishment of an adult home range are generally important for homing ability. Although the evidence is admittedly circumstantial, the fact that the same initial pathway was often followed in subsequent releases of successfully homing animals on the golf course and that movements were more rapid suggests that an animal need traverse an area one time whereupon the homing pathway is familiar and apparently learned. This is evident in the recaptures of 11 of the 12 successfully homing animals when released more than one time on the golf course and the return of several within a matter of hours. In this connection, Harrison (1958) concluded that *Rattus* was able to learn homing routes and that subsequent release of successfully homing animals at the same point of liberation results in a much higher percentage of returns. A similar trend can be found in the work of Murie and Murie (1931), Rawson (1956), Feniuk and Popova (1940), and Schleidt (1951), each of whom recorded higher homing returns from subsequent releases of successfully homing mice. The contention that learning and memory do play a role in homing ability is further supported by the present retention experiments, in which mice seemed to recognize their home ranges and were remarkably successful in homing with or without experimental experience prior to laboratory isolation. It seems possible, therefore, that cotton mice learn and retain for extended periods of time a memory of the terrain encountered during dispersal (environmental imprinting) and subsequently use this means (mnemotaxis) in homing.

The results reported in this paper by no means identify the particular sensory mechanisms utilized in homing. Visual cues may be important. Bodenheimer and Kornhauser (1955) have shown that wild mice have the ability to discern visual differences and to utilize them in learning a situation. However, other sense modalities such as auditory and chemical senses probably also play a role. It appears likely

that by utilizing the ordinary senses mice are capable of learning and retaining for prolonged periods of time a schema of their near and more distant environments and to utilize this familiarity in homing activity.

Further, it seems appropriate to suggest that psychic factors are important in a consideration of home range and homing. Based on the degree of psychological attachment to an area, small rodents may be considered to have three types of zones: 1) Territory, as defined by Burt (1943), which is the defended part of the home range; 2) Home Range, or a zone of intimate familiarity and close affinity; and 3) Life Range, or a zone of general familiarity gained as a result of dispersal, occasional wandering, and home range shifts. Homing from within the life range is assumed to be a nonrandom activity with respect to the homesites, whereas homing from beyond the life range, hence from totally unfamiliar territory, is probably by means of random wandering until familiar terrain is encountered.

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A Study of Lichen Ecology in Central Long Island, New York¹

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ABSTRACT: The epiphytic lichens of eleven forest stands in central Long Island were sampled by the random pair method and the stands are arranged in a continuum based on their epiphytic flora. This continuum exhibits certain discontinuities resulting in ecologically different segments.

The distributions of the common lichens along this continuum gradient are analyzed. Most lichens are shown to have their greatest frequency in the mature oak woods. It is suggested that if moisture and light are recognized as important factors in lichen distribution on a local level, the mature oak woods can be regarded as a point of compromise between the dry but well lighted pine-oak barrens and the moist but poorly lighted sub-climax woods.

The host-specificities of the eight common lichens for Black Oak, White Oak, and Pitch Pine are analyzed using Cole's Index of Inter-specific Association and significance tests. *Parmeliopsis placodioides* was extremely specific for *Pinus rigida*; *Graphis scripta*, *Lecanora leptyrodies*, and *Parmelia saxatilis* were highly specific for Black Oak. It is noted, however, that the host-specificities in one vegetation type sometimes differ from those in other vegetation types.

This study was undertaken to expand our knowledge of the lichens of Long Island. The area is especially interesting floristically because of its unusual geographic position; the northern limit of the southeastern coastal plain element overlaps the southern limits of several northern elements. Although the central and eastern portions of the island still exhibit a rich and varied lichen flora, little collecting has occurred since the 1920's and 30's when Roy Latham was especially active. The lichens of the western portion of the island have mostly disappeared due to urbanization, and only scattered herbarium specimens and literature reports attest to their former prominence.

The specific aims of the study were (1) to determine the ecological niches of the common lichens of the area; (2) to determine the host-specificities of the common lichens for the area; (3) to set up permanent quadrats for a long term growth rate project, and (4) to secure floristic data on the lichens of central and eastern Long Island.

Since much work is still to be done on the growth rate and floristic studies, they will be discussed at some future time. This paper is confined to the ecological investigations.

¹ This study was supported by a New York State Museum and Science Service Graduate Study Honorarium for Summer Research.

² Contribution No. 60-18 from the Department of Botany and Plant Pathology, Michigan State University, East Lansing, Michigan.

Acknowledgments.—I sincerely thank Dr. Eugene C. Ogden, the New York State Botanist, for helping me procure living and working facilities for the duration of the study. Thanks also go to Dr. Albert W. Herre who identified all the specimens of *Usnea* and Dr. Mason E. Hale, Jr., who identified many of my early collections. Miss Constance Nagle of the Meteorology Group at Brookhaven National Laboratory kindly supplied a compilation of climatological data. A special debt of gratitude is owed Dr. Henry A. Imshaug who verified or identified almost all the specimens collected, and who helped in the preparation of the manuscript. Many thanks are due Drs. John Cantlon, Philip J. Clark, and Thomas Eisner for their suggestions and criticisms.

HISTORY

At the turn of the century, when "botanizing" was a popular pastime and collecting a favorite hobby, Long Island became a popular area for study. In 1899, S. E. Jelliffe published "The Flora of Long Island" which listed 54 lichen taxa. In particular he studied Flushing, Jamaica, New Lots, Valley Stream, Cold Spring Harbor, Orient, Young, and Montauk (see Fig. 1). At that time, *Cladonia uncialis* was abundant in Brooklyn (now one of the most heavily populated parts of New York City) and *Cetraria islandica* dotted the now residential Richmond Hill section of Queens in New York City. Wood (1905) published additions to the lichen flora adding 18 taxa to Jelliffe's list. In 1914, Wood published a list of the lichens growing in the vicinity of New York City and included many species from Long Island.

About 1910, Roy Latham began to collect extensively in eastern Long Island. In collaboration with S. H. Burnham, he published "The Flora of the Town of Southold, Long Island" in 1914. Burnham and Latham listed 140 lichen taxa in this major contribution to our knowledge of the lichens of eastern Long Island. Latham continued his collecting and published a series of notes on his observations of *Cetraria islandica* (Latham, 1945, 1946, 1947) and one on *Cladonia alpestris* (Latham, 1949). His specimens have been widely distributed, but no résumé of his findings have been published.

The area around Cold Spring Harbor on the north shore of the island was studied by Grier in 1925. During the first few decades of the century, Raymond Torrey led many trips in connection with the Torrey Botanical Club, and published various accounts of his observations. Typical of the short, informal, but often important notes is his paper on the Rock Tripes of Long Island (Torrey, 1933).

Babette Brown Coleman's study on the epiphytes of New York (Brown, 1948) included some observations of Long Island lichens. No papers dealing with the Long Island lichen flora have appeared since 1949.

GENERAL DESCRIPTION OF THE STUDY AREA

The major vegetation types of central Long Island (Suffolk County) were sampled from Wildwood State Park on the north shore

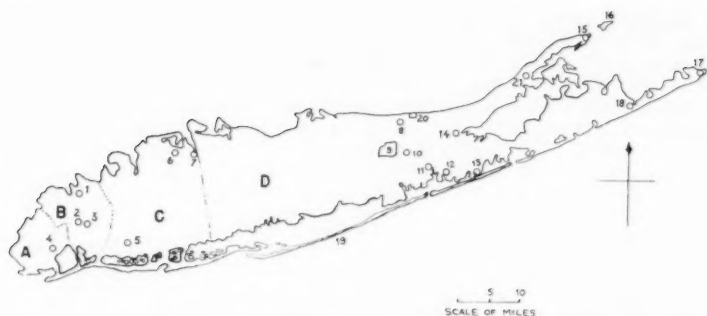


Fig. 1.—Distribution of localities on Long Island, N. Y. Counties: A—Kings (Brooklyn, New York City); B—Queens (N.Y.C.); C—Nassau; D—Suffolk. Towns, parks, etc.: 1—Flushing; 2—Richmond Hill; 3—Jamaica; 4—New Lots; 5—Valley Stream; 6—Oyster Bay; 7—Cold Spring Harbor; 8—Wading River; 9—Brookhaven National Laboratory (B.N.L.); 10—Manorville; 11—Eastport; 12—Speonk; 13—Quogue; 14—Riverhead; 15—Orient; 16—Plum Island; 17—Montauk Point; 18—Promised Land; 19—Fire Island (Sunken Forest State Park); 20—Wildwood State Park; 21—Southold.

to Westhampton Beach on the south shore, and from Brookhaven National Laboratory east to the Manorville area. Some collections were also made on the southeastern "point" of the island near Promised Land and Montauk Point, and on Fire Island near Sunken Forest State Park (Fig. 1).

Four more or less distinct terrestrial vegetation types could be recognized within the study area: sand barrens, pine-oak barrens, mature pine-oak woods, and sub-climax woods. A few bogs also occur in the area.

The vegetation of the sand barrens formed on dune-sands (Fuller, 1914), and common along the south shore, consists primarily of *Hudsonia tomentosa*,³ *Ammophila breviligulata*, and *Myrica pennsylvanica*, with a dense mat of many *Cladoniae* covering the loose sand. In the sand barren areas near the ocean, such as the one studied on Westhampton Beach in Quogue, large sand dunes dominate the area and a characteristic vegetation pattern results. A hypothetical cross-section of one of the dunes appears as depicted in Figure 2. Lichens are most abundant at the base of the lee side of the dune and in the hollows where the wind is slight. *Cladonia submitis* is by far the dominant lichen over the flats and extends far up the lee side of the dune until the brush becomes dense and little light reaches the ground. Large patches of *Cladonia boryi* and *C. uncialis* are scattered over the barrens, especially towards the base of the dune.

³ All phanerogamic nomenclature is from Fernald (1950).

Nearly circular cushion-shaped clumps of *C. boryi* were observed over large areas of totally exposed sand. Each clump was centered over the dead stump of a dune-grass plant apparently having gained its original foothold there. This may explain how slow-growing lichens can colonize a loose-sand habitat. Thus, the classical successional sequence of lichen-moss-grass-brush, is more or less reversed in this case. The hardy dune-grass is the pioneer, followed by lichens which gain a foothold on the decaying but stabilized grass stump, and this is followed by other xeric phanerogams which require some accumulated organic matter for colonization and depend on the decaying grasses and lichens for this material.

Lecidea uliginosa creates abundant tar-like patches on the bare sand of sand barrens further inland such as the one on Old Country Road near Speonk. These sand barrens are formed not on dune sand but rather on sandy outwash material from the Ronkonkoma moraine (Fuller, 1914). Associated with it are large sprawling specimens of *Cladonia cristatella*.

Pine-oak barrens represent the major vegetation type of central Long Island. They consist of mixed stands of *Pinus rigida*, *Quercus alba*, *Q. ilicifolia*, and a few other xeric oaks. The ground cover is mainly *Vaccinium* spp. No ground lichens are conspicuous with the exception of *Baeomyces roseus* which covers many bare eroded banks of the fire breaks criss-crossing the area. The soil is sandy and has little accumulated organic matter.

The pine-oak barrens grade into the mature pine-oak woods which are also common on the island. Along with large Pitch Pines and White Oaks, Black Oak (*Quercus velutina*) becomes important. As is shown below, this formation displays the richest epiphytic lichen flora. Many extensive patches of ground-dwelling *Cladoniae* such as *Cladonia subtenuis* and *C. uncialis* appear in this community



Fig. 2.—Hypothetical cross section through a "typical" sand dune at Quogue, L.I.

where there is an opening in the canopy and sunlight reaches the ground. The soil is much like that of the pine-oak barrens.

The fourth vegetation type, the sub-climax woods, was observed only on the north shore at Wildwood State Park. It has many characteristics of a typical climax forest such as sparse ground cover, thick leaf litter, and large trees. The trees, however, are mostly *Quercus velutina* and *Acer rubrum* and not typically representative of climax vegetation. Lichens are relatively rare in this formation, with a corticolous flora of mostly crustose species such as *Graphis scripta*, and without any ground lichen flora.

Three different type bogs were briefly studied. One of them (Bog A) is located on Old Country Road near Speonk (Fig. 3). It is shallow and filled with *Sphagnum* and decayed stumps, and supports many characteristic bog plants such as *Drosera rotundifolia*, *Lycopodium inundatum*, *Utricularia* spp., and *Kalmia angustifolia*. *Cladonia atlantica* was the most abundant of the several lichen species collected on the hummocks formed by the stumps.

Another bog (Bog B), formed in a gravel pit, was found just off Old Country Road near Eastport (Fig. 3). The water is extremely shallow and a tree layer is absent. The bog supports a lush growth of *Drosera rotundifolia* and *Lycopodium* spp. Around the edge of the bog, especially the northern edge, thick colonies of *Cladoniae* were

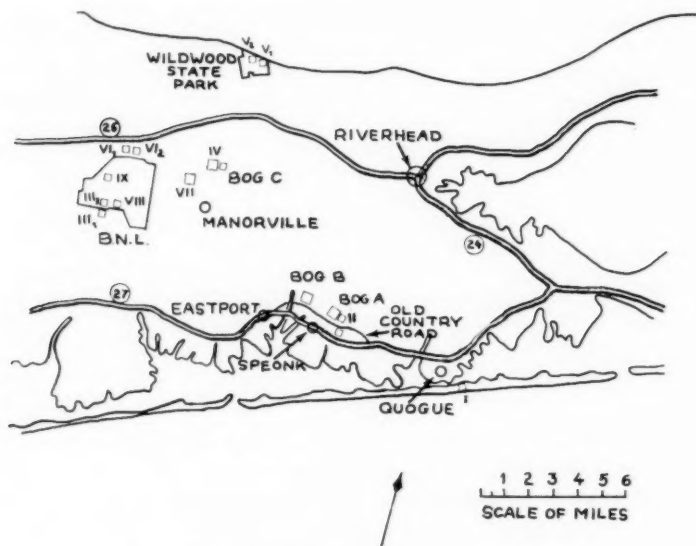


Fig. 3.—Map of central Long Island showing specific stands and areas studied.

found consisting mainly of *C. subtenuis*, *C. atlantica*, *C. uncialis*, and *C. caroliniana*. Many of the patches were growing in mats of *Polytrichum* sp. which were wet with bog water.

The third bog (Bog C), just southeast of Stand IV (Fig. 3), consists of an extensive shallow lake and a swampy adjacent area which had been used for cranberry cultivation. *Drosera* spp. and *Utricularia* spp. are abundant, and *Cladonia atlantica* and *C. subtenuis* are common at the bog edge.

CLIMATE

The climate of central Long Island falls into the "Dfa" category of Köppen's climatological classification system (Köppen, 1941). The rainfall distribution is constant throughout the year averaging four inches per month except for the dry months of June and July.

Central Long Island is rather windy with over half the days in the year having winds between 11 and 18 mph. During the summer, the prevailing winds are from the southwest; during the winter, they are from northwest.

The average temperature from May 1st to September 30th is 64.6° F, and from October 1st to April 30th, it is 39.6° F. The temperature rarely goes above 90° or below 10° F.

METHODS

Thirteen areas were selected for study including several examples of each major vegetation type. Areas I and II were treeless sandbarrens. Areas III₁, III₂, IV, V₁, V₂, VI₁, VI₂, VII, VIII, IX, and X were wooded and were studied for their epiphytic lichen flora. Each of these wooded areas will be referred to as "stands" in the following discussions. It was unfortunately not possible to restrict this study to undisturbed areas as was done in the Wisconsin studies of Hale (1955) and Culberson (1955) since almost all the wooded sections of central Long Island are "disturbed" to some degree. This study, therefore, cannot be compared with the Wisconsin studies without taking this important difference into account. An effort was made, however, to select the more undisturbed stands.

When a stand had been chosen, a 40 tree sample was taken by the "random-pair" method described by Cottam and Curtis (1949). (The correction in technique mentioned by Curtis in a later paper (Cottam and Curtis, 1955) was not used in this study.) Care was taken to avoid the edges of the woods where road effects, different light and moisture conditions, etc., might influence the data. All trees with a diameter at breast height (dbh) of 6 cm or more were studied for their epiphytic lichen flora. Observations were made on two quadrats girdling the trunk, base and breast height, in an effort to include most of the common species: (1) one quadrat was 30 cm high from the ground-level; (2) another quadrat was 40 cm high centered at 1.3 meters from the base. No notes on abundance

TABLE I.—Kulczynski's coefficient of community; each value indicates the degree of similarity between a pair of stands based on their lichen flora; the higher the coefficient, the greater is the degree of similarity.

	III ₁	III ₂	IV	V ₁	V ₂	VI ₁	VI ₂	VII	VIII	IX	X
III ₁		72	37	4	13	70	61	21	68	50	35
III ₂			38	5	13	65	75	33	81	62	50
IV				18	22	45	52	56	43	58	50
V ₁					53	5	4	14	7	24	18
V ₂						22	20	19	18	28	24
VI ₁							65	28	75	54	44
VI ₂								44	76	76	55
VII									33	46	59
VIII										68	49
IX											53
X											

or coverage were taken in this study since the presence or absence of a particular species were the only points under consideration.

Identifications were made in the field. Any questionable specimen however was numbered and collected, and later identified in the laboratory. Because of the time factor, the only crustose lichens studied were those which could be reliably identified in the field.

CONTINUUM GRADIENT

In order to understand the distributional behavior of lichens, recent writers (Hale, 1955; Culberson, 1955) have studied the distribution of some common lichens along a "continuum" (Curtis and McIntosh, 1951) of forest types, a linear ecological arrangement of stands based on their tree composition. In those studies, the continuum was set up by an involved set of computations involving tree densities, dominance factors, and a "climax adaptation number".⁴

Because of the small number of stands examined (only eleven) and their similarity in tree composition (almost all contain *Pinus rigida*, *Quercus velutina*, and *Q. alba*), setting up a continuum according to the above method would have been impractical. The existence of a continuum can hardly be questioned, but here we have one which can best be demonstrated by including important factors that are more subtle than mere tree frequency. By analyzing the lichen composition of each stand, a continuum can be constructed which seems to reflect a linear order of ecological development. This continuum was constructed by comparing pairs of stands by Kulczynski's "coefficient of community" (Culberson, 1955). A matrix of values was constructed (Table I) from which visual analysis

⁴ A numerical value assigned to each tree species according to its autecological position in Wisconsin relative to *Quercus macrocarpa* (C.A. No. 1) which is a tree common to pioneer formations, and *Acer saccharum* (C.A. No. 10) the dominant climax forest tree.

and considerable shuffling enabled the arrangement of the stands into a linear order according to similarity and dissimilarity of the lichen composition.

The coefficient of community is a "measure of the level of similarity for any pair of communities from a set of quantitative measurements taken for both" (Culbertson, 1955). It can be represented

by the formula $\frac{2w}{a + b} \times 100$ where a = the sum of the frequencies

of a set of lichen species in one association, b = the sum of the frequencies of the lichen species of the other association, and w = the sum of the frequencies of the lichen species which are shared by both associations (using, of course, the lower frequency in each case as being the maximum possible shared frequency). The frequencies are expressed as percentages to permit comparisons.

By visual analysis, the following continuum series was constructed:

III₁ III₂ VI₁ VIII VI₂ IX IV X VII V₂ V₁

The most pioneer stands are at the left and the ones closest to climax are at the right.

In the process of arranging the stands into a continuum series,

TABLE II.—General characteristics of four segments of the continuum

Segment	Dominant tree or trees	Dominant ground cover	Light conditions*	Soil	Average dbh (in centimeters)		
					<i>Pinus rigida</i>	<i>Quercus velutina</i>	<i>Quercus alba</i>
Segment A	<i>Quercus alba</i> , <i>Pinus rigida</i>	<i>Quercus ilicifolia</i> , <i>Vaccinium</i> spp., <i>Pteridium aquilinum</i>	Excellent-good	very sandy	10.1	8.7	8.3
Segment B	<i>Pinus rigida</i> , <i>Quercus alba</i> , <i>Q. velutina</i>	<i>Vaccinium</i> spp., <i>Pteridium aquilinum</i>	Good	sandy	13.7	12.3	10.2
Segment C	<i>Quercus velutina</i>	<i>Vaccinium</i> spp., <i>Pteridium aquilinum</i>	Good	sandy	18.5	14.9	10.9
Segment D	<i>Quercus velutina</i>	<i>Parthenocissus quinquefolia</i> , <i>Viburnum acerifolium</i>	Fair	thick, moist, leaf litter	22.5	15.9

* Excellent: at least ¼ the area in open sunlight, the rest in moderate shade.
Good: less than ¼ the area in open sunlight, the rest in moderate shade.
Fair: no open sunlight falling on ground, some sunlight filtering through the trees.

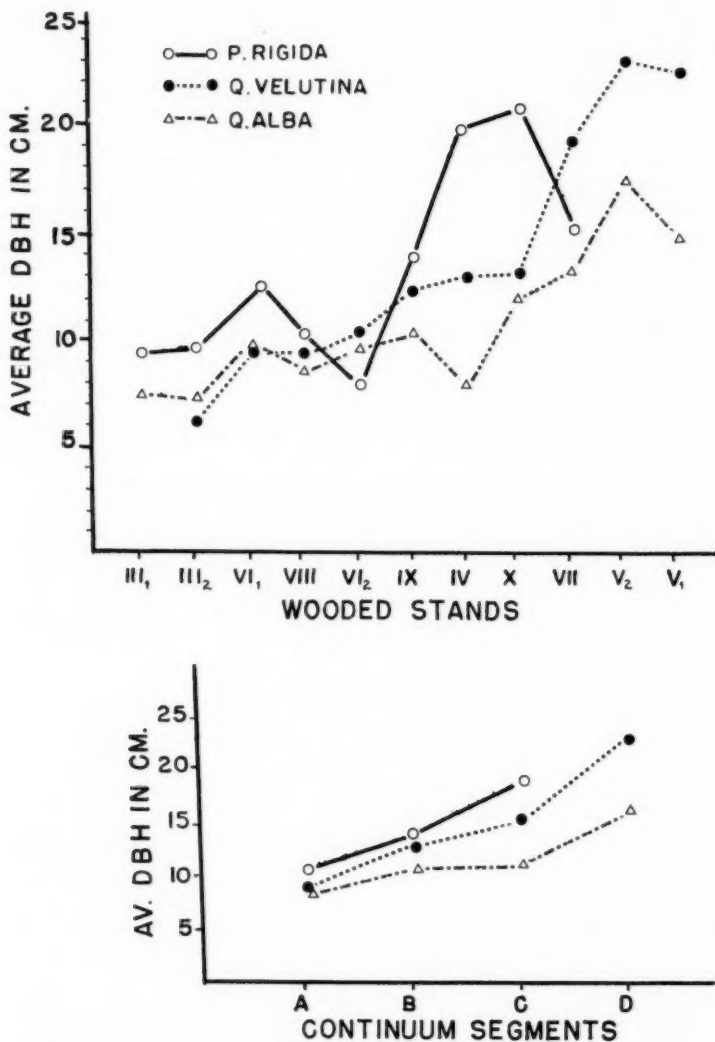


Fig. 4.—Average diameter-breast-height (dbh) of three common species of trees (*Pinus rigida*, *Quercus velutina*, *Q. alba*) along the continuum.

it was noted that the stands fell into four more or less distinct groups, almost certainly due to the small number of stands examined and the fact that the stands were originally selected to give as great a variation in vegetation type as possible. The continuum was divided into segments as follows:

III ₁	III ₂	VI ₁	VIII	VI ₂	IX	IV	X	VII	V ₂	V ₁
		A			B		C		D	

It was difficult to decide on the status of Stand VI₂, but it was finally included with Segment A after much shuffling and deliberation. The other groups are rather well defined. We can classify them as follows: Segment A = pine-oak barrens, Segment B = young pine-oak woods, Segment C = mature pine-oak woods, and Segment D = sub-climax woods. The main features of these segments are

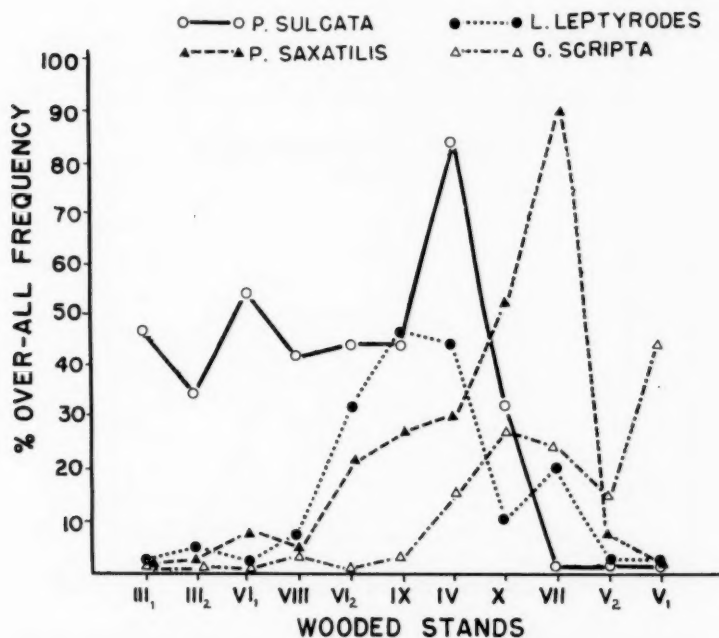


Fig. 5.—The frequencies of four common lichen species (*Parmelia sulcata*, *P. saxatilis*, *Lecanora leptyroides*, *Graphis scripta*) along a continuum of wooded stands.

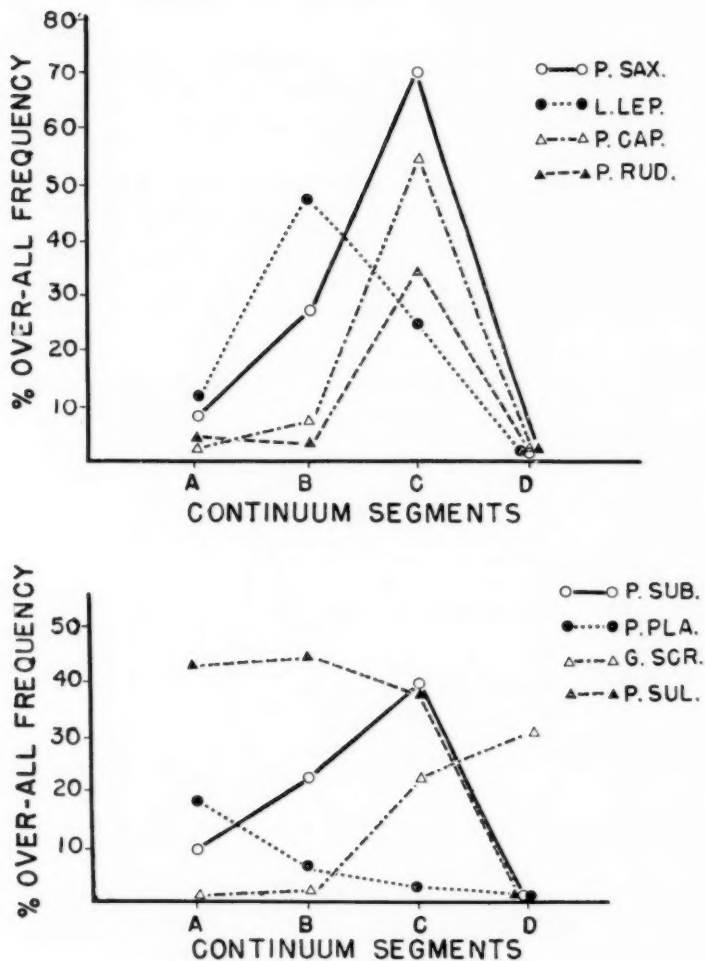


Fig. 6.—The frequencies of the eight common lichen species along the four continuum segments. (P. sax = *Parmelia saxatilis*, L. lep. = *Lecanora leptyroides*, P. cap. = *Parmelia caperata*, P. rud. = *Parmelia rudecta*, P. sub. = *Parmelia subaurifera*, P. pla = *Parmeliopsis placorodia*, G. scr. = *Graphis scripta*, P. sul. = *Parmelia sulcata*.)

summarized in Table II. Note the regular patterns which can be seen in the increase of dbh (Fig. 4), the rise and fall of light conditions, and the change of subdominants from pioneer to climax communities.

It is unfortunate that so irregular a grouping had to be made. Although the difference in number of trees represented by each continuum segment will no doubt necessitate qualifications in the conclusions drawn from its use, the arrangement gives us a more or less accurate picture of the actual situation.

Using the continuum as a framework, it is possible to plot the

TABLE III.—Frequencies of some corticolous lichens
of central Long Island

	Tree occurrence, % of 440 trees	% of total quadrat occurrences (2 quadrats per tree)	
		Basal quadrat	1.3m quadrat
<i>Cladoniae</i> *	26	88	12
<i>Graphis scripta</i>	12	23	77
<i>Lecanora subfusca</i> (group)	18	23	77
<i>Lecanora leptyroides</i>	16	24	76
<i>Lecidea anthracophila</i>	3	52	48
<i>Parmelia caperata</i>	16	56	44
<i>Parmelia perforata</i>	4	100
<i>Parmelia physodes</i> = <i>Hypogymnia physodes</i>	7	44	56
<i>Parmelia rudecta</i>	12	69	31
<i>Parmelia saxatilis</i>	22	60	40
<i>Parmelia subaurifera</i>	18	15	85
<i>Parmelia subquercifolia</i>	9	13	87
<i>Parmelia sulcata</i>	34	27	73
<i>Parmeliopsis aleurites</i>	5	20	80
<i>P. placorodia</i>	10	17	83
<i>Physcia millegrana</i>	9	7	93
<i>P. orbicularis</i>	6	52	48
<i>P. stellaris</i>	6	15	85
<i>Usnea strigosa</i>	3	22	78

* *Cladoniae* = both identified and unidentifiable material. The values here represent averages of the data collected for the epiphytic members of this genus.

frequency of the more common lichens (those with an over-all frequency of 10% or more) (see Table III) along the continuum to discover where the species are most important. Figure 5 shows the distribution of four lichens which demonstrate four major distribution patterns. When the continuum is divided into four segments (Fig. 6), we find that the distribution patterns of most of the common species fit one pattern type with a few important exceptions.

Graphis scripta frequency rises from pioneer toward climax communities. *Parmelia sulcata* does the opposite starting at a peak and dropping to zero per cent frequency in the sub-climax stands. It is interesting to note the distribution of *P. sulcata* as compared to that of the closely related *P. saxatilis*. Notice that the two patterns begin as almost exact opposites in the pine-oak barrens, then both show a peak in the mature pine-oak woods (significantly in different stands), and together fall to a zero point in the sub-climax (see Fig. 5).

VERTICAL DISTRIBUTION

Table III presents frequencies of lichens at the tree-base level and 1.3 meters from the base, as well as their total frequencies. From this information, we can classify the *Cladoniae* (including *C. cristatella* and the *C. chlorophaea* group) as being usually found in the basal area, and *Graphis scripta*, *Lecidea anthracophila*, *Lecanora leptyroides*,⁵ *Parmelia subquercifolia*,⁶ *P. subaurifera*, and *Parmeliopsis placodioides* as being rarely, if ever, found in the basal zone. The other species seem to show no consistent vertical distribution and probably vary in position according to the immediate light and moisture conditions. Vertical distributions of corticolous lichens and bryophytes have been studied by Charles C. Plitt (1924), Billings and Drew (1938), Hale (1952), Barkman (1958), and Brodo (1959). All these workers have emphasized the importance of moisture and light on vertical distribution of cryptogams.

MOISTURE-HOLDING CAPACITY AND pH OF BARK SUBSTRATES

Moisture-holding capacities and pH of the barks of various tree species were examined in many of the stands in which they occurred to see if the bark characteristics of any species would vary under different environmental conditions. No significant differences could be found between barks of the same species in different communities.

⁵ This species, here reported for the first time for North America, was apparently included in *Lecanora pallida* var. *angulosa* (= *L. carpineae*) by Fink (1935). *L. leptyroides* and *L. carpineae* both differ from *L. pallida* by having a C+ (orange) reaction on the apothecial disks. A cortex is present on the apothecial margin in *L. carpineae* but is absent in *L. leptyroides*.

⁶ Dr. Mason E. Hale, Jr., has recently informed me that the American material of *Parmelia subquercifolia* actually represents both *P. livida* Tayl. & *P. galbina* Ach. and that both species are represented in my Long Island material.

TABLE IV.—Cole's index of interspecific association as applied to a lichen and its supporting tree; a value of +1 indicates perfect association, and -1 indicates perfect dissociation.

SEGMENT A				
	No. occurrences	<i>Pinus rigida</i> 70**	<i>Quercus velutina</i> 28	<i>Quercus alba</i> 79
<i>Graphis scripta</i>	1	-1.0	-1.0	+1.0
<i>Lecanora leptyroides</i>	21	-1.0*	+ .72*	— .34
<i>Parmelia caperata</i>	7	-1.0	+ .17	+ .53
<i>P. rudecta</i>	6	-1.0	+ .61*	— .16
<i>P. saxatilis</i>	16	-1.0*	+ .35	+ .28
<i>P. subaurifera</i>	20	-1.0*	+ .07	+ .67*
<i>P. sulcata</i>	86	-1.0*	+ .56*	+ .69*
<i>Parmeliopsis placorodia</i>	37	+1.0*	-1.0*	-1.0*
SEGMENT B				
	No. occurrences	<i>Pinus rigida</i> 11	<i>Quercus velutina</i> 15	<i>Quercus alba</i> 13
<i>Graphis scripta</i>	1	-1.0	+1.0	-1.0
<i>Lecanora leptyroides</i>	19	-1.0*	+ .49*	+ .27
<i>Parmelia caperata</i>	3	-1.0	+ .47	+ .01
<i>P. rudecta</i>	1	-1.0	+1.0	-1.0
<i>P. saxatilis</i>	11	-1.0*	+ .71*	— .44
<i>P. subaurifera</i>	9	-1.0	+ .29	+ .18
<i>P. sulcata</i>	18	-1.0*	+ .39	+ .30
<i>Parmeliopsis placorodia</i>	3	+1.0*	-1.0	-1.0
SEGMENT C				
	No. occurrences	<i>Pinus rigida</i> 16	<i>Quercus velutina</i> 65	<i>Quercus alba</i> 28
<i>Graphis scripta</i>	27	-1.0*	+ .84*	-1.0*
<i>Lecanora leptyroides</i>	30	-1.0*	+ .56*	— .71*
<i>Parmelia caperata</i>	62	-1.0*	+ .33*	+ .11
<i>P. rudecta</i>	41	-1.0*	+ .36*	+ .08
<i>P. saxatilis</i>	69	-1.0*	+ .28*	+ .50*
<i>P. subaurifera</i>	49	-1.0*	+ .44*	+ .002
<i>P. sulcata</i>	46	-1.0*	+ .38*	— .55
<i>Parmeliopsis placorodia</i>	4	+1.0*	-1.0	-1.0*
SEGMENT D				
	No. occurrences	<i>Pinus rigida</i> 0	<i>Quercus velutina</i> 39	<i>Quercus alba</i> 16
<i>Graphis scripta</i>	25	+ .45*	-1.0*
<i>Lecanora leptyroides</i>	0
<i>Parmelia caperata</i>	0
<i>P. rudecta</i>	3	+1.0	-1.0
<i>P. saxatilis</i>	0
<i>P. subaurifera</i>	0
<i>P. sulcata</i>	0
<i>Parmeliopsis placorodia</i>	0

* Significance value at the five per cent level.

** Number of individual trees examined.

TABLE V.—The values presented below represent the probabilities (in per cent) of calling particular associations significant when they are in reality, insignificant.

SEGMENT A			
	<i>Pinus rigida</i>	<i>Quercus velutina</i>	<i>Quercus alba</i>
<i>Graphis scripta</i>	60-70	80-90	40-50
<i>Lecanora leptyroides</i>	.05-.10	.00-.05	10-20
<i>Parmelia caperata</i>	5.0-10	20-30	10-20
<i>P. rudecta</i>	5.0-10	.10-.50	.95-1.0
<i>P. saxatilis</i>	.50-1.0	.10-.50	20-30
<i>P. subaurifera</i>	.10-.50	50-60	.00-.05
<i>P. sulcata</i>	.00-.05	.00-.05	.00-.05
<i>Parmeliopsis placorodia</i>	.00-.05	1.0-2.5	.00-.05
SEGMENT B			
	<i>Pinus rigida</i>	<i>Quercus velutina</i>	<i>Quercus alba</i>
<i>Graphis scripta</i>	70-80	40-50	60-70
<i>Lecanora leptyroides</i>	.05-.10	2.5-5.0	30-40
<i>Parmelia caperata</i>	50-60	50-60	80-90
<i>P. rudecta</i>	70-80	60-70	60-70
<i>P. saxatilis</i>	2.5-5.0	.05-1.0	20-30
<i>P. subaurifera</i>	2.5-5.0	10-20	30-40
<i>P. sulcata</i>	.05-.10	5.0-10	20-30
<i>Parmeliopsis placorodia</i>	.00-.05	50-60	50-60
SEGMENT C			
	<i>Pinus rigida</i>	<i>Quercus velutina</i>	<i>Quercus alba</i>
<i>Graphis scripta</i>	1.0-2.5	.00-.05	.10-.50
<i>Lecanora leptyroides</i>	.50-1.0	.10-.50	1.0-2.5
<i>Parmelia caperata</i>	.00-.05	.50-1.0	60-70
<i>P. rudecta</i>	.10-.50	1.0-2.5	60-70
<i>P. saxatilis</i>	.00-.05	.50-1.0	1.0-2.5
<i>P. subaurifera</i>	.10-.50	.05-.10	80-90
<i>P. sulcata</i>	.10-.50	.10-.50	5.0-10
<i>Parmeliopsis placorodia</i>	.10-.50	2.5-5.0	1.0-2.5
SEGMENT D			
	<i>Pinus rigida</i>	<i>Quercus velutina</i>	<i>Quercus alba</i>
<i>Graphis scripta</i>		1.0-2.5	.50-1.0
<i>Lecanora leptyroides</i>			
<i>Parmelia caperata</i>			
<i>P. rudecta</i>		10-20	60-70
<i>P. saxatilis</i>			
<i>P. subaurifera</i>			
<i>P. sulcata</i>			
<i>Parmeliopsis placorodia</i>			

HOST-SPECIFICITY

Some lichens have a much higher probability of being found on certain tree species than on others. In two recent papers (Hale, 1955; Culberson, 1955), this "host-specificity" was statistically demonstrated for certain lichens using Cole's Index of Interspecific Association (Cole, 1949). Cole's Index measures the degree of association between two independently varying species, in this case, the tree "host" and the lichen. The index is so constructed that a value of +1 indicates perfect association, -1 indicates perfect dissociation, and zero indicates that one species is associated with the other no more than would be expected by probability when both are randomly distributed.

Dissociation and association indicated by Cole's Index were tested for significance at the five per cent level using Chi-square and, where appropriate, Fisher's direct method (Fisher, 1950). The raw data were used in applying the tests. The Cole's Indices for the eight common corticolous lichens are presented in Table IV and the significance values presented in Table V. The data have been broken down into the four ecological groups (continuum segments) because it has been shown (Brodo, 1959) that host-specificity varies significantly under different ecological conditions.

In the present study, it is also possible to see the variation in specificity of a lichen from one group to another. Although it would be possible to construct a graph demonstrating these changes, it would lead to certain misleading conclusions because of the natural variations in the index number caused by differences in numbers of lichen and host occurrences. Instead, a set of five categories was set up based on the significance and lack of significance of the associations and dissociations over the four continuum segments. The following statements delimit the categories and present the theoretical status of the lichens as to host-specificity.

Category *a*: Lichens having a significantly high Cole's Index wherever it and the host have been found in "reasonable abundance." In this study, reasonable abundance was considered to be a frequency of five per cent or more, the figure is probably a little low, and in larger samples might be raised to 10 per cent. These species show true host-specificity in the area studied indicating possible host requirements.

Category *b*: Lichens whose indices are significantly high under some conditions and are insignificantly high or low under other conditions. These species have some specificity for the tree host, but have no clear-cut requirements for it.

Category *c*: (1) Lichens whose indices show both significant associations and dissociations, or (2) show no significant associations or dissociations at all, under various conditions. No lichens were observed to have fallen into group (1) which is as would be expected. Several species, however, could be included in group (2). Lichens in this category would seem to be most flexible in their substrate requirements, varying in degree of association with any particular tree species as the bark characteristics

such as texture, chemistry, and moisture relations change in the different stands.

Category *d*: Lichens whose indices are significantly low in some continuum segments and insignificantly high or low in others. These lichens may have some tolerance for the normally unfavorable substrate, but will occur more abundantly on other more favorable trees, if they are available.

Category *e*: Lichens having a significantly low Cole's Index wherever it and the tree are found in reasonable abundance. They have some sort of physical or physiological inability to inhabit that substrate.

Eight common lichen species were placed in the above categories according to their distribution on the three common trees (see Table VI). It must be kept in mind that an ordinarily significant association or dissociation may appear to be insignificant in an excessively small sample. (In categorizing the lichen species in Table VI, the only index values considered were those based on at least a 5% frequency of occurrence for the lichen in a given continuum segment.) For example, placing *Parmeliopsis placorodia* in category *d* with *Quercus velutina* and *Q. alba* may be misleading. There was a lack of significance in its dissociation with the oaks in Segment B where it was only found three times (a frequency of 7.5%). In a larger sample, the lichen would almost certainly have shown significant dissociations with the oaks and would have therefore been placed in category *e*. As a matter of fact, this species was never observed by the author on Long Island on any substrate other than Pitch Pine. Culbertson (1954) found that in the more northern parts of the country, *Parmeliopsis placorodia* is found on *Pinus banksiana* (Jack Pine), but never on hardwoods, and this has been the personal experience of the writer in the field. However, for the most part, the table presents a good idea of the substrate behavior of the common lichens.

From Table VI, we see that besides the high specificity of *Parmeliopsis placorodia*, for Pitch Pine, *Graphis scripta*, *Lecanora leptyroides*, and *Parmelia saxatilis* are highly specific for Black Oak, although, unlike *Parmeliopsis placorodia*, they are not confined to

TABLE VI.—Degrees of host-specificity of the eight most common corticolous lichens for the three dominant trees; categories based on data in Table IV: *a* = constant positive specificity; *b* = some positive specificity; *c* = no specificity; *d* = some negative specificity; *e* = constant negative specificity.

	<i>Pinus rigida</i>	<i>Quercus velutina</i>	<i>Quercus alba</i>
<i>Graphis scripta</i>	<i>e</i>	<i>a</i>	<i>e</i>
<i>Lecanora leptyroides</i>	<i>e</i>	<i>a</i>	<i>d</i>
<i>Parmelia caperata</i>	<i>d</i>	<i>b</i>	<i>c</i>
<i>P. rudecta</i>	<i>e</i>	<i>a</i>	<i>c</i>
<i>P. saxatilis</i>	<i>e</i>	<i>a</i>	<i>b</i>
<i>P. subaurifera</i>	<i>d</i>	<i>b</i>	<i>b</i>
<i>P. sulcata</i>	<i>e</i>	<i>b</i>	<i>b</i>
<i>Parmeliopsis placorodia</i>	<i>a</i>	<i>d</i>	<i>d</i>

one tree species. In general, Black Oak appears to be the "best" substrate for the lichens in the areas studied, and *Pinus rigida* the poorest.

DISCUSSION

CONTINUUM GRADIENT

An analysis of the total flora of a stand can tell us more about the position of the stand in a continuum than can an analysis of the tree composition alone. It is also clear that the more pertinent parameters used in arranging any group of stands in a linear order, the more meaningful the order becomes. Of course, the more parameters introduced into a formula, the more cumbersome the formula becomes and calculations are made impractical. Lichen distributions have been shown in many ecological studies (Hale, 1952, 1955; Culberson, 1955; Barkman, 1958) to be influenced by many of the same environmental conditions which we would like to include in our formula, such as size of trees, available light, and humidity, besides the important factor of tree composition. By working with lichen distribution, therefore, one would be "automatically" including these parameters in the formula.

However, the use of coefficient of community values and trial and error juggling to fit the values into a linear sequence, immediately limits the number of stands one can conveniently work with. For a study such as this one covering a relatively small area with a small number of stands, especially where the tree composition is fairly constant, this method of continuum analysis is most valuable. For larger stand samples with greater variety in tree composition, the standard Curtis and McIntosh method would probably be better.

With the continuum constructed on the basis of lichen composition, lichen distribution patterns along the gradient are very similar in some ways to those seen by Hale (1955) in his study of the upland forests of southern Wisconsin. The peak in abundance of lichen species in oak woods and the sharp drop in abundance in climax forests which he observed corresponds to the peak in pine-oak woods and drop in sub-climax seen in this study. Even the exception to this general rule, that of *Graphis scripta* which rises steadily to a peak in the climax-type communities, was observed.

An important difference in the continuum, however, is in the relative position of *Quercus alba*-dominated stands. In previous studies in Wisconsin (Curtis and McIntosh, 1951; Hale, 1955), *Quercus velutina* was considered a pioneer forest tree and *Quercus alba* was considered to be a tree characteristic of woods closer to climax. In this study, the positions are reversed; that is, *Q. alba* is clearly associated with *Pinus rigida* (the ecological equivalent of *Pinus banksiana* in Wisconsin) in primitive pine-oak barrens, and *Quercus velutina* is most abundant in association with such typical climax trees as *Carya* spp. and *Ostrya virginiana*. It is possible that climatic differences between Wisconsin and Long Island or more probably differences in the biotypes of the Black and White Oaks in the two areas

produce this lack of consistency, although no definite explanation can be offered at this time.

Although it is not difficult to find patterns of distribution for most of the species studied, it is almost impossible to make any definite statements as to the causes of specific patterns. If a lichen has a host-specificity for a particular tree species, we can predict that the lichen distribution will follow more or less closely the distribution of its host (as we saw with *Parmeliopsis placododia*). However, we can also see that specificity changes under different ecological conditions (see Table IV). These changes in specificity were noted by the writer between poorly and well-drained stands in central New York (Brodo, 1959).

It has been stated that light and humidity have an effect on lichen distribution (Plitt, 1924; Degelius, 1935; Hale, 1952; Barkman, 1958). The great abundance of lichen flora in the mature pine-oak woods probably reflects that vegetation type's position as a "compromise" point between the abundant light and extreme dryness of the pine-oak barrens and the poor light and moist conditions of the sub-climax woods. Minerals (Almborn, 1948) and salt spray (Degelius, 1935) also have their effects and may be exerting important influences on distribution especially in the sub-climax stands which are overlooking Long Island Sound (see Fig. 3). These factors are difficult, if not impossible to separate in the study area.

An interesting puzzle in distribution has been presented by two common *Parmeliae*, *P. sulcata* and *P. saxatilis*. These are closely related species with similar chemistries and morphologies. In fact, the two can only be separated by a careful examination of the thallus for the presence of isidia or soredia; *P. saxatilis* has isidia and no soredia, while *P. sulcata* has soredia and no isidia. If, in the process of speciation, the two became distinct physiologically as well as morphologically, one would expect them to inhabit entirely different niches. Figure 4 shows that for the most part, they are not found together and seem to have different ecological requirements. However, a very interesting point can be seen within continuum segment C (one of the more uniform communities). In one stand, *P. sulcata* reaches its peak, and in another it is almost absent; where *P. sulcata* is absent, *P. saxatilis* shows its peak. The two stands (IV and VII) which are within 1½ miles of each other, have very similar ecologies. There would appear to be a significant difference between the two stands, but one which so far has eluded the writer.

Graphis scripta presents a somewhat different problem. While it shows a high specificity for *Quercus velutina*, its occurrence does not closely follow that of its host particularly in continuum segment B. (See Fig. 6 and Table IV). The reasons are not clear, but it is possible that the size of the trees involved, and the resulting dissimilarities in bark characteristics, as was mentioned by Billings and Drew (1938), as well as the humidity and light conditions characteristic of progressively more "climax" forests, caused the variation.

HOST-SPECIFICITY

The data presented in this paper point to the need for caution in discussing host-specificity. It has been shown that the specificity of a lichen for a tree will vary with the ecological conditions. Thus, it is important to remember that when we speak of "the host-specificity of *Parmelia sulcata* for *Quercus velutina*," we may really mean, the specificity of the lichen for Black Oak in a dry, mature pine-oak woods, in a pine barren, etc., in central Long Island. The geographical consideration mentioned above is very important. In order to discover something about the host-lichen relations for a particular lichen species, it would be necessary to sample the forests throughout the normal range of the lichen. *Parmeliopsis placorodia* is a good case in point. The species is limited to the northeastern United States with few exceptions. In Long Island, it is found only on *Pinus rigida* which would lead us to believe that the lichen has an absolute specificity for this tree. However, as was mentioned previously, *P. placorodia* is found abundantly on *Pinus banksiana* in the northern pine barrens. It would be indeed interesting to study the host-specificity of this lichen in northern New England where the ranges of Jack Pine and Pitch Pine overlap.

The reasons for host-specificity are complicated and difficult to determine experimentally. It is believed that in certain cases, the physical and chemical bark characteristics such as moisture-holding capacity, texture, pH, and mineral composition have much to do with it (Billings and Drew, 1938; Hale, 1952 and 1955; Culbertson, 1955; Barkman, 1958; Brodo, 1959). In certain highly specific lichens, especially the more primitive crustose forms, the bark may even contribute to the nutrition of the thallus (Fink, 1913; Johnson, 1940). It is impossible to make any definite statements concerning host-lichen relations at this time, although I am studying this intriguing problem to some extent.

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The Geographic Variation of *Ambystoma macrodactylum* Baird, with the Description of Two New Subspecies¹

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ABSTRACT: The taxonomic history of the salamander *Ambystoma macrodactylum* is briefly reviewed. The recently described race *A. m. croceum* is accepted. Certain differences in color and color pattern of adult animals, especially as concern the dorsal band, indicate the existence of four additional races: *A. m. columbianum* and *A. m. sigillatum*, heretofore unrecognized subspecies; *A. m. krausei* and *A. m. macrodactylum*, restricted and redefined. For each subspecies, description, distinguishing characteristics, distribution, variations or known local deviants and a list of specimens examined are presented. Sexual dimorphism of the vent is described.

Specimens of the four races are pooled into four samples and the means of 14 ratios formed from measurements and counts are compared using a completely randomized Factorial Design, the Analysis of Variance and the Individual Degree of Freedom based on the *F* distribution. A number of significant differences are demonstrated, lending additional support to the taxonomic separation of the species into the proposed races. A key to adults of the subspecies is given.

Life history data pertaining to breeding, larval development and habitat preferences are presented and compared for the various races.

INTRODUCTION

Since Baird's (1849) original description of the long-toed salamander from specimens obtained near Astoria, Oregon, the validity of the species has been widely recognized. On three occasions, certain populations of *A. macrodactylum* have been assigned species rank only to be placed in synonymy by later authorities. Peters (1882) applied the name *Ambystoma kraussii* to Flathead River, Montana specimens which he believed to differ from *macrodactylum* in dorsal band color. Cope (1883) rejected *kraussii* but described *Ambystoma epixanthum* from the South Boise River in Idaho, again on the basis of band color and certain meristic variations. Ruthven (1912) applied the name *A. stejnegeri* to four specimens supposedly collected near Bloomfield, Davis County, Iowa. Ruthven held that the Iowa animals could be distinguished from *macrodactylum* by toe length and tail morphology. Additional specimens from the Iowa locality have not been reported and it seems likely that the original locality data were in error.

More recently, Mittleman (1948) reported on the geographic variation of *Ambystoma macrodactylum* and separated the species into two allopatric races as follows: "*A. m. macrodactylum* Baird ranges

¹ Based on a thesis presented to Oregon State College in partial fulfillment of the requirements for the Doctor of Philosophy degree.

from the Columbia Plateaus province and the northern Basin and Range province in Washington and Oregon, through the Cascade-Sierra province and Pacific Border province from Calaveras County, California to southeastern British Columbia. The other race, *A. m. krausei* Peters, is known definitely from the Northern Rocky Mountain province in Idaho and Montana, and from southwestern Alberta and British Columbia as far west as Kamaloops, and probably north to Lat. 58°; it has been recorded also from Iowa."

The diagnostic features presented by Mittleman for the two races are as follows: 1) total vomerine count (67% of sexually mature *macrodactylum* with 34 or more; 75% of sexually mature *krausei* with less than 33); 2) ratio of head width to snout-vent distance (more than the value of

$$\frac{(2 \log SV)^2 - (\log SV)^2}{SV}$$

in 65% of *macrodactylum*; less than that value in 85% of *krausei* specimens); 3) ratio of head width to head length (69.5% or more in 74% of *macrodactylum* and 69.4% or less in 75% of *krausei*). In addition, the races were presumed to differ with respect to certain stable color differences.

The "subspecies" defined by Mittleman cannot be diagnosed on the basis of his "key characters." For example, although he indicates that 67 per cent of mature Oregon and Washington *macrodactylum* have vomerine counts of 34 or more, in the present study, 79.3 per cent of 222 specimens from western Oregon and Washington had 33 or less vomerine teeth. Also, in contrast to 75 per cent of Mittleman's Idaho specimens having 33 or less vomerine count, only 30.8 per cent of the 26 present study Idaho specimens had this "character." Discrepancies in the two sets of data might result from two conditions. First, and most important, Mittleman examined only a single specimen from western Oregon (Baird's type) and 75 of his 87 Oregon specimens were from Crater Lake. Second, there is a slight possibility of discrepancy because Mittleman used only specimens measuring 40 mm or more from snout to *posterior* angle of the vent and the present study used animals measuring 38 mm or more from snout to *anterior* margin of the vent.

When Mittleman's ratios were applied to specimens from the entire range of the species, they failed to prove diagnostic. Moreover, his color differences, apparently based solely on preserved material, were found to be inadequate for identification of living animals.

Recent workers have not accepted Mittleman's races. Stebbins (1951) states regarding the separation, "In my opinion there is too great overlap in the characters submitted as criteria for recognition of these races. The color differences presented are unconvincing." Schmidt (1953) omitted reference to subspecies in his checklist. Bailey (1948) criticized certain of Mittleman's statistical methods, and Mittleman (1949) has subsequently published a defense of them. Ferguson (1952a) found considerable variation between *macro-*

dactylum from western Oregon and northeastern Oregon, the latter having a more pronounced dorsal stripe after preservation, larger spots on the head, more irregular edges to the stripe and a darker ground color. In view of the confusion concerning the status of the races, the present study was initiated to re-examine the problem in light of new material obtained in the last several years.

After the present study was in progress, Russell and Anderson (1956) reported a new race, *A. m. croceum*, from near Rio Del Mar in Santa Cruz County, California. This locality is nearly four hundred miles south of the recognized coastal range of *macrodactylum* and one hundred and fifty miles southwest of the nearest Sierra Nevada populations, from which it is separated by the Great Valley of California. Although *croceum* was not included in the present study, living specimens in the possession of Russell and Anderson were examined. The pattern, color differences, and widely disjunct range clearly indicate the merit of recognizing this subspecies.

Acknowledgments.—A large number of people have contributed in one way or another to the completion of this study. The following persons have loaned specimens in their care: Mr. C. M. Beatty, Glacier National Park; Dr. Royal Bruce Brunson, Montana State University; Dr. G. Clifford Carl, Provincial Museum of British Columbia; Dr. Doris M. Cochran, United States National Museum; Dr. Philip C. Dumas, University of Idaho; Mr. J. M. Broadbent, Crater Lake National Park; Dr. Robert C. Stebbins, University of California; Dr. Kenneth Walker, College of Puget Sound. The following people contributed living specimens: Dr. Donald S. Farner, Washington State College; Dr. James Kezer, University of Oregon; Dr. David Jameson, San Diego State College; Dr. Charles W. Quaintance, Eastern Oregon College; Dr. Robert M. Storm, Oregon State College; Mr. Oliver W. Johnson, Oregon State College.

Mr. Richard Russell and Dr. James D. Anderson of the University of California kindly supplied me with a copy of their unpublished manuscript concerning *A. m. croceum* and offered many helpful suggestions as has Dr. Robert C. Stebbins of that institution. Dr. Jerome C. R. Li has very patiently advised and helped me with the statistical analyses. Dr. Richard A. Pimentel (California State Polytechnical College) and Dr. James D. Anderson read the manuscript and offered helpful suggestions. To all of these people I am most grateful.

Finally, I should like to express my sincerest appreciation to Dr. Robert M. Storm, who directed the study.

DESCRIPTION OF THE SUBSPECIES

Ambystoma macrodactylum columbianum subsp. nov.

Eastern Long-toed Salamander (Fig. 1)

Diagnosis.—An *Ambystoma macrodactylum* with: 1) a dorsal band width exceeding the internarial distance; 2) an uninterrupted band on the body that is not deeply incised; 3) band pigment on the head, snout and eyelids in the form of large, well-defined spots; 4) a combined vomerine count exceeding 33; 5) see the section on statistical analyses for other useful diagnostic characters.

Type.—USNM 142228, an adult female, collected August 3, 1956 near a small lake located 0.5 mile N. Anthony Lakes (SW $\frac{1}{4}$, Sec. 7, R37E, T7S), Union Co. Oregon, (Elev. 7100 feet) by Oliver W. Johnson and Denzel E. Ferguson.

Paratypes.—USNM 142229-142246.

Distribution.—Lake County and the Deschutes drainage of Oregon, north through the Cascades of Oregon, Washington and British Columbia and east to the Bitterroot Mountains of Idaho; north through central British Columbia to S. Alaska (Fig. 2).

Description of Type (from living anesthetized specimen).—Maximum width of band on body, 5.8 mm; length from snout to anterior margin of vent, 58.3 mm; vent to tip of tail, 56.6 mm; head width, 11.2 mm; head length, 14.9 mm; length of right front leg, 15.4 mm; axilla to groin length, 27.3 mm; span of hind legs, 43.2 mm; inter-narial distance 3.7 mm; vomerine teeth, 36 in four groups (7, 10, 12, 7); costal grooves 13, counting one each in axilla and groin.

Dorsal stripe Wax Yellow (Capitalized color terms after Ridgway, 1912) and sharply demarcated from the black background color; the stripe is uninterrupted on the body, with a single interruption on the tail, and extends to within 3 mm of the tail tip; four patches of ground color are isolated in the band; edges of the band on the body slightly undulated with pronounced lobulations extending laterally on the tail; each eyelid provided with a large patch of band pigment; other large, well-defined patches on the head and snout; isolated patches of band color present on the lateral surfaces of the tail and upper limb surfaces; guanophores present ventral to the level of the upper eye, being smaller and fewer in number on the tail, and most abundant on the gular region, body and limbs; guanophores near the tops of the costal grooves assume the color of the band pigment; a large reddish-gold patch in the upper half of the eye; two small patches in the lower half.

Variation.—The stripe color of *columbianum* varies from bright yellow to tan, frequently appearing metallic. Although the dorsal



Fig. 1.—A specimen of *Ambystoma macrodactylum columbianum* n. ssp. from the type locality in Union Co., Oregon. Body length 58 mm; total length 107 mm.

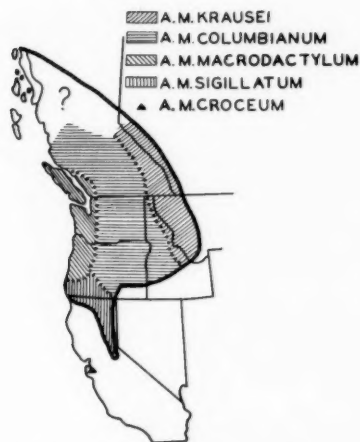


Fig. 2.—The distribution of the races of *Ambystoma macrodactylum* omitting Iowa records.

stripe is always sharply delimited from the ground color, the edges are variable, ranging from nearly parallel to irregularly indented. Large clearly defined patches of ground color are isolated in the band of some specimens but absent in most. Certain adults have a dorsal stripe more or less continuous onto the snout and the large, well-defined smooth-edged spots on the head may appear diffuse in young. The conspicuous spots of band pigment, often present on the lateral tail surfaces, are generally absent in other races. Band pigment lateral to the band and on limb surfaces is not as extensively developed as in *krausei*. The guanophores of *columbianum* are the most conspicuous found in the species. Ventral coloration may be dark chocolate in color but is lighter than the dorsal ground color.

The eye pigment is nearly always confined to the upper half of the eye, being most dense on the periphery. When pigment occurs in the lower half, it forms clumps rather than being evenly dispersed. The eye pigment of young animals is scattered throughout the eye.

Certain specimens from the Palouse area of southeastern Washington possess band characteristics differing from the typical *columbianum* pattern and approaching those of *macrodactylum*. However, the meristic characters and vomerine counts of these specimens conform to those of *columbianum*.

Specimens Examined.—IDAHO: Bonner Co. (2); Idaho Co. (6); Kootenai Co. (10); Latah Co. (18); Valley Co. (4). OREGON: Baker Co. (3); Deschutes Co. (4); Grant Co. (2); Lake Co. (3); Umatilla Co. (10); Union Co. (117); Wallowa Co. (24); Wasco Co. (14); Wheeler Co. (2). WASHINGTON: Asotin Co. (3); Chelan Co. (12); Columbia Co. (1); Douglas Co. (20); Garfield Co. (3); Grant Co. (2); King Co. (4); Kittas Co. (5); Klicki-

tat Co. (4); Lewis Co. (2); Lincoln Co. (11); Okanogan Co. (2); Pende Orielle Co. (4); Pierce Co. (3); Spokane Co. (7); Stevens Co. (5); Walla Walla Co. (1); Whatcom Co. (10); Whitman Co. (4); Yakima Co. (12). CANADA: British Columbia—Okanogan Landing (2); Kamalloops (1); Lac le Jeune (3); Telegraph Creek (1); Tetana Lake (2); Manning Park (1).

***Ambystoma macrodactylum sigillatum* subsp. nov.**

Southern Long-toed Salamander (Fig. 3)

Diagnosis.—Similar to *A. m. croceum* but with 1) bright yellow dorsal markings (Wax Yellow, Sulphine Yellow, Aniline Yellow, Lemon Chrome); 2) dorsal band often interrupted, forming smooth-edged spots or at least deeply incised, its maximum width being less than the internarial distance; 3) band pigment on head and snout in small distinct dots; 4) combined vomerine count exceeding 33; 5) see the section on statistical analyses for other useful diagnostic characters.

Type.—USNM 142212, an adult female, collected July 28, 1956 100 yards W. of the boat landing in Eagle Cove of Crater Lake, Klamath Co., Oregon, (Elev. 6170 feet) by Oliver W. Johnson and Denzel E. Ferguson.

Paratypes.—USNM 142213-142227.

Distribution.—Western Oregon south of the Calapooya divide, the southern Cascades of Oregon in the vicinity of Crater Lake, the Klamath drainage basin and south in the Sierra Nevada range to Calaveras Co., California (Fig. 2). Dr. James D. Anderson (personal communication) has recently obtained records in Tuolumne Co., thus extending the range somewhat farther south.

Description of Type (from living anesthetized specimen).—Maximum width of band on body (widest spot), 2.8 mm; length from snout to anterior margin of vent, 60.9 mm; vent to tip of tail, 54.0 mm; head width, 11.6 mm; head length, 14.9 mm; length of right front leg, 14.1 mm; axilla to groin length, 31.7 mm; span of hind legs, 40.1 mm, internarial distance 4.2 mm; vomerine teeth, 44 in four groups (7, 15, 14, 8); costal grooves 13, counting one each in axilla and groin.

Dorsal stripe Wax Yellow, sharply demarcated from the black

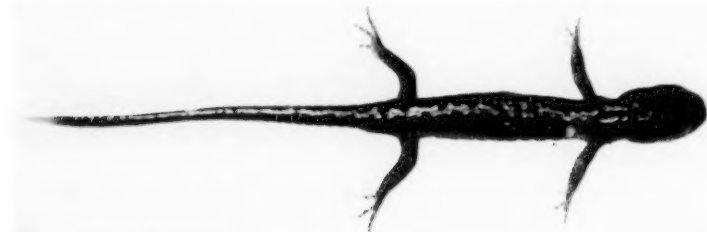


Fig. 3.—An *Ambystoma macrodactylum sigillatum* n. ssp. from the type locality, Crater Lake, Crater Lake National Park, Oregon. Body length 66 mm; total length 124 mm.

ground color; dorsal stripe extends from the level of the gular fold to within 10 mm of the tail tip, with three interruptions on the body and several on the tail; the stripe represented on the head and snout by tiny well-defined flecks; dorsal stripe narrow with irregular edges; stripe pigment absent on the limbs but some guanophores on the upper limb surfaces and sides of the abdomen show a yellow tinge; guanophores present on the snout and all areas ventral to a line extending through the upper eye, but are smaller and fewer in number on the tail; guanophores on sides of abdomen and upper limb surfaces tend to coalesce; an unconsolidated, silver guanoid patch in the upper half of the eye has a red tinge.

Variation.—The dorsal stripe of *sigillatum* is always bright yellow, being the brightest of all the races. The stripe on the body is typically narrow and may be formed of a series of well-defined spots, or quite continuous and deeply incised. On the head, posterior to the eyes, the band pigment may form definite spots, but appears as smaller, distinct flecks or dots on the snout. The undersides are usually sparsely pigmented with a light network of melanophores and frequently appear translucent in life (with a pinkish cast, or blue where internal organs show through the body wall) and whitish gray in preservation.

The eye pigment forms a gold to silver patch, with a red tint caused by superficial blood vessels, and is confined to the upper half in adults. Small quantities of pigment may occur in the lower half of the eye in young.

A. m. sigillatum examined from the Sierras in California have a wider band than do Oregon specimens. The band may be interrupted to form a series of large, transversely arranged, smooth-edged spots. When not actually interrupted, the band may have deep undulations which nearly break through as noted by Russell and Anderson (1956). Certain specimens from the west side of Klamath Lake in Oregon resemble Sierran material. Although the Sierran population differs from typical *sigillatum*, I am inclined to view the variation as being clinal, with one extreme located near Crater Lake in Oregon and the other at the southern extremity of the species' range in the Sierra Nevada of California. Future study and more material may demonstrate the Sierran population to be distinct. At the present, in view of existing similarities and an apparently continuous geographic distribution, it seems best not to attempt separation. Russell and Anderson (*op. cit.*) recognized this problem in stating that the affinity of *croceum* seemed more likely with Crater Lake populations than with those of the Sierras.

In view of the fact that a race of newts, *Taricha granulosa mazamae*, is known to be endemic to the Crater Lake caldron, the possibility of similar local subspeciation in *Ambystoma macrodactylum* was examined. However, *sigillatum* dwelling in the caldron were indistinguishable from those in other nearby lakes and in the Rogue River Valley.

Specimens Examined.—CALIFORNIA: Alpine Co. (3); Calaveras Co. (1); Eldorado Co. (1); Plumas Co. (2). OREGON: Douglas Co. (10); Jackson Co. (27); Klamath Co. (118).

Ambystoma macrodactylum croceum Russell and Anderson
Santa Cruz Long-toed Salamander

For the sake of uniformity, the following description of the holotype of *A. m. croceum* from Rio Del Mar, Santa Cruz Co., California is included (after Russell and Anderson, 1956): "(from living anesthetized animal). Length from snout to anterior margin of vent, 57.2 mm.; from vent to tip of tail, 51.0 mm.; head width, 9.5 mm.; head length, 13.9 mm.; vomerine teeth, 33, in four groups (6, 9, 11, 7) forming a transverse arc behind the internal nares; costal grooves 13, counting one each in axilla and groin.

Ground color black, consisting of heavily concentrated melanophores; pattern on the back a series of eleven small orange patches; this light pigment represented by tiny dots on head and a nearly continuous stripe along crest of tail; guanophores absent dorsally, concentrated as a band of silvery flecks dorsolaterally along a line connecting the limb insertions and extending forward onto the upper surfaces of cheeks and forelimbs; guanophores fewer on hind limbs and lateral surfaces of tail, widely scattered on belly; upper half of eye with a guanoid patch given a pinkish cast by associated blood vessels; this eye color lost after preservation".

Identifying characteristics for *croceum* are a dull orange dorsal band (between Pekinese and Raw Sienna), a tendency for the band to be broken up into a number of discrete spots, and a reduced dorsal head pattern which consists of scattered dots, that are often absent anterior to the eyes.

The race *croceum* is known only from Santa Cruz County, California (Fig. 2).

Although *croceum* was not studied, it should be pointed out that it could only be confused with *sigillatum*, and only then if distribution was unknown for a salamander in question. The two races are easily separated by band color (Raw Sienna in *croceum*, yellow in *sigillatum*) and a more discontinuous band and darker ground color in *croceum*.

Ambystoma macrodactylum krausei Peters
Northern Long-toed Salamander (Fig. 4)

On the basis of the present study, the name *krausei* is restricted to *A. macrodactylum* having the following distribution: Bitterroot Mountains of eastern Idaho, throughout western Montana and north through western Alberta and eastern British Columbia (east of the Selkirk Mountains) to Jasper National Park (Fig. 2). Specimens from Valley and Idaho Counties in central Idaho show a *krausei* influence in having a band more continuous onto the head and are considered to be intergrades with *columbianum*.

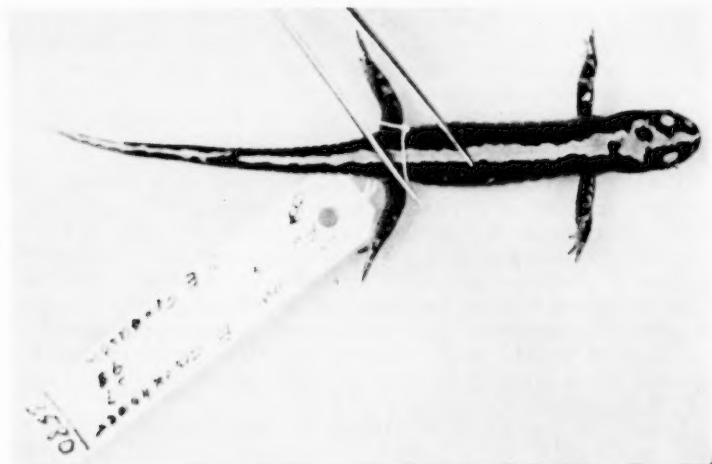


Fig. 4.—A specimen of *Ambystoma macrodactylum krausei* from 11 miles east of Eisenhower Forks, Banff National Park, Alberta, Canada. Body length 57 mm; total length 98 mm.

The following description pertains to a representative specimen of *krausei* (from living anesthetized animal): Oregon State College MNH 3580, an adult male collected July 7, 1955 about 11 miles E. of Eisenhower Forks, Banff National Park, Alberta, Canada by Denzel E. Ferguson.

Maximum width of band on body, 3.2 mm; length from snout to anterior margin of vent, 49.3 mm; vent to tip of tail 47.7 mm; head width, 8.8 mm; head length, 12.2 mm; length of right front leg, 13.9 mm; axilla to groin length, 30.2 mm; span of hind legs, 40.1 mm; internarial distance 3.0 mm; combined vomerine count, 31; costal grooves 12, counting one each in axilla and groin.

The dorsal band is Aniline Yellow at midbody becoming darker on the ridge of the tail. Near the stripe at midbody, the ground color is between Aniline Black and black. The dorsal stripe is narrow, starting at the mouth line and extending to within 2 mm of the tail tip with but a single interruption on the tail. The stripe is expanded immediately posterior to the eyes at which point a large patch of ground color is isolated within the band. Each eyelid has a large well-defined spot of band pigment. The edges of the band are nearly parallel and abruptly separated from the surrounding ground color. On the body, a dozen or so patches of band color are isolated lateral to the band proper, and many large distinct patches of band pigment are present on the dorsal surfaces of both fore and hind limbs.

Guanophores are present on the sides of the snout and lateral

surfaces of the body (up to the level of the dorsal edge of the eye), becoming more sparse laterally on the tail. Guanophores on the body near the band assume a tinge of the band color. Smaller guanophores are abundant ventrally and are sometimes clumped to form larger white patches. Guanophores are lacking on the dorsal limb surfaces but present on the lips of the vent.

Variation.—The ground color of *krausei* is often conspicuously darkened adjacent to the band. Isolated ground color is seldom seen in the band, although the dorsal stripe of two specimens of a series from Glacier National Park, Montana, is broken into spots similar to those of *sigillatum* and *croceum*. Guanoid pigment of the eye is silver or gold with a red tint and is often absent entirely. In young, the pigment may appear gray and is evenly dispersed throughout the eye. *Krausei* is very dark ventrally due to a dense melanophore network. Ruthven's type for *stejnegeri* has been examined and found to fit *krausei* as here described.

Identifying characters for *krausei*: 1) band continuous onto the snout and widest in the vicinity of the eyes; 2) band yellow and uninterrupted; 3) large patch of band color on each eyelid; 4) band narrow and the edges nearly parallel; 5) combined vomerine count less than 34; 6) see statistical analyses for other characters of value.

Specimens Examined.—IOWA: (?) Davis Co. (1). MONTANA: Flathead Co. (21); Glacier Co. (1); Lake Co. (8); Missoula Co. (30); Ravalli Co. (18); Sanders Co. (8). CANADA: Alberta—Eisenhower Forks (3). British Columbia—Cranbrook (1); Echo Lake (8); Kootenai Crossing (5); Mount Monashee (10).

Ambystoma macrodactylum macrodactylum Baird

Western Long-toed Salamander (Fig. 5)

The nominate race, as here defined, includes *A. macrodactylum* populations west of the Cascade Mountains, extending from the Calapooya divide in Oregon, north through western Oregon and Washington and along the coast of British Columbia to a point opposite the northern tip of Vancouver Island, including Vancouver Island and other offshore islands (Fig. 2).

The following is a description of a representative specimen of *A. m. macrodactylum* (from living anesthetized animal): Oregon State College MNH 3985, an adult male collected April 10, 1956 near Corvallis, Benton Co., Oregon by Denzel E. Ferguson. Maximum width of band on body, too diffuse and indistinct to measure; length from snout to anterior margin of vent, 50.3 mm; vent to tip of tail, 47.4 mm; head width, 9.0 mm; head length, 11.4 mm; length of right front leg, 15.3 mm; axilla to groin length, 26.0 mm; span of hind legs, 39.8 mm; internarial distance, 2.92 mm; combined vomerine count, 30; costal grooves, 13, counting one each in axilla and groin.

The dorsal band is between Citrine and Dark Citrine at mid-body, changing to Dull Citrine on the tail. The ground color at

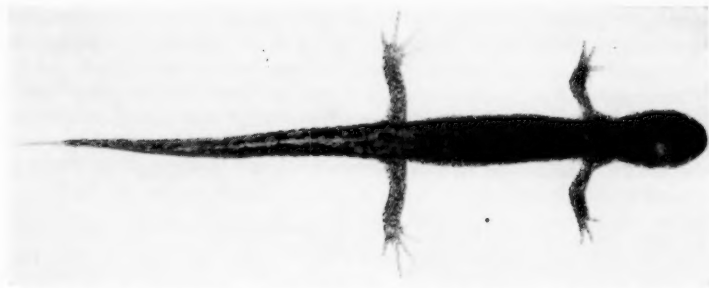


Fig. 5.—An example of *A. m. macrodactylum* collected near Corvallis, Benton County, Oregon. Body length 56 mm; total length 104 mm.

midbody approaches Dark Quaker Drab. The band is very diffuse in appearance, and forms a gradual transition into the ground color making it impossible to say where one begins and the other stops. A tint of ground color is evident throughout the band. Anterior to the gular fold, the stripe is absent, but represented by a very diffuse "wash" of band pigment, which consists of extremely irregular scattered flecks. Band pigment on the eyelids is also of this diffuse nature. The edges of the band are formed by a dispersion of band pigment, similar to that described for the head, which almost imperceptibly changes into a dense concentration of guanophores on the lateral surfaces of the body. These guanophores are extremely numerous coalescing in a manner to give the sides a solid whitewashed appearance. This dense concentration of guanophores extends ventrally from the level of the eyes to a line connecting the fore and hind limb bases, below which they gradually become fewer and separated. Scattered guanophores appear on the gular region, limb surfaces and lower halves of the lateral tail surfaces. The eye pigment consists of green or red tinged golden flecks, mainly in the upper half of the eye (most concentrated near the edge of the pupil), but with scattered patches in the lower half as well.

Variation.—In life, the band of adult *macrodactylum* is drab (usually Dull Citrine or Dark Citrine) but often approaches bright yellow in recently metamorphosed young. In aquatic, breeding adults and after preservation, the band of Willamette Valley specimens may be so indistinct as to appear absent at a first glance. Band pigment is frequently absent from the upper limb surfaces and never conspicuous if present. Guanophores extend higher on the sides in this race than in others, and fewer melanophores give it a lighter ground coloration, especially on the ventral aspects. Eye pigment of young is dispersed throughout the eye.

Some specimens of *macrodactylum* from the Olympic Peninsula area of western Washington have a more distinct band, approaching that of *columbianum*. However, their meristic characteristics and

vomerine counts are those of *macrodactylum*. The coloration and pattern of Baird's type, although difficult to discern, show a tendency toward *columbianum*. A possible explanation may be a *columbianum* gene flow through the Columbia River Gorge, since some larvae and adults are no doubt washed downstream and adults accidentally transported with debris. A single specimen from Columbia Co., Oregon displayed similar evidence of the *columbianum* race in its band characteristics.

Identifying Characters for macrodactylum.—1) dorsal stripe dull in color (citrine), appearing very diffuse on the head, snout, eyelids and edges of the band; 2) guanophores reaching to the dorsal extremities of the costal grooves and coalesced to give the sides a whitewashed appearance; 3) light gray ground color with tinges of brown in preservation; 4) combined vomerine count less than 34; 5) head short and narrow; 6) see statistical analyses for other characters of value.

Specimens Examined.—OREGON: Benton Co. (101); Clatsop Co. (1, Baird's type); Columbia Co. (1); Lane Co. (21); Linn Co. (100); Polk Co. (4). WASHINGTON: Callam Co. (8); Cowlitz Co. (4); Gray Harbor Co. (7); Island Co. (1); King Co. (6); Kitsap Co. (2); Lewis Co. (5); Mason Co. (8); Pierce Co. (35); Skamania Co. (8); Snohomish Co. (2); Thurston Co. (2). CANADA: British Columbia—Hope (12); Vancouver Island (4); Huntingdon (1).

INTERGRADATION

Exact statements concerning the nature and extent of intergradation between the races of *Ambystoma macrodactylum* must await additional study based on intensive collecting in suspected zones of contact. However, examination of available collections has helped to clarify the problem in at least a few significant areas. The subspecies *sigillatum* and *columbianum* are known to intergrade where they meet along a fairly restricted zone through Klamath and Lake Counties in south-central Oregon (Fig. 2). Specimens from this area possess the wider dorsal stripe of *columbianum* but have the characteristic interrupted pattern of *sigillatum*.

Intermediates between *sigillatum* and *macrodactylum* are not known. Present data indicate their geographic ranges to be disjunctly allopatric, the Calapooya Divide, in west, central Oregon, being the possible point of separation.

No *macrodactylum* records are available from the western slope of the Oregon and Washington Cascade Mountains, and it is doubtful that they will be forthcoming. However, the distribution of *columbianum* extends up the eastern slope to the crest of the range. This apparently disjunct pattern of distribution would appear to preclude genetic interchange between *macrodactylum* and *columbianum* along the Cascade barrier. However, as mentioned above, *columbianum* influence via the Columbia River Gorge is apparent in *macrodactylum* populations from areas along the lower Columbia River in north-

western Oregon. Specimens from southwestern British Columbia, along the Frazier River drainage in the area east of Vancouver, also appear to be intergrades between these two races.

A fairly broad zone of intergradation between *columbianum* and *krausei* runs parallel to the Bitterroot and Selkirk ranges, beginning in central Idaho and extending northward through western British Columbia. Salamanders from Bonners Ferry, Idaho are definitely intermediates and impossible to allocate to subspecies. The identity of the subspecies occupying northern British Columbia and southern Alaska is not known for certain, there being only a few poorly preserved specimens available from the region. Those examined more closely approach *columbianum* than any other race.

LARVAE AND YOUNG

Large numbers of *columbianum* and *macrodictylum* larvae were examined but consistent differences were not found. However, there is a tendency toward a darker coelom lining and a higher gill raker count in *columbianum*. Immatures cannot be assigned to their subspecies on the basis of diagnostic adult characters. Recently metamorphosed young of all subspecies exhibit bright dorsal stripes (Strontium Yellow, Wax Yellow, Oil Yellow, Amber Yellow, Olive Ochre, Deep Colonial Buff), important band characteristics are not evident, and vomerine counts are not reliable.

SEX DETERMINATION

The sex of breeding long-toed salamanders is usually established by examination of the vent. However, in rare instances, dissection and examination of the gonads might be necessary. In general, the vent of breeding males is extremely bulbous due to enlargement of the cloacal lips, while the cloacal lips of females form a much smaller cone-like protuberance. The vent of the male is more heavily pigmented with melanophores and has a long opening that is lined by protuberant flaps of tissue bearing rows of papillae. In females the cloacal lip pigment is sparse or lacking, the vent is shorter and the inside lining is grooved or ridged in place of being papillate. Vent dimorphism is considerably more pronounced in *macrodictylum* than in *columbianum* or *sigillatum* but only slightly more so than in *krausei*. Dr. James D. Anderson (personal communication) has pointed out that *croceum* shows strong vent dimorphism, approaching that of *macrodictylum*.

STATISTICAL ANALYSES

Only animals measuring 48.5 mm or more snout to vent were used in the statistical analyses. Measurements were taken with Vernier calipers and read to the nearest one-tenth millimeter, except as otherwise specified below. Contorted or poorly preserved animals were forcibly flattened, if possible, or otherwise omitted. The following information was taken from each specimen:

1) length of right front leg—the distance from the tip of the longest toe to the point of limb attachment to the body;

2) head length—the distance from the tip of the snout to the gular fold;

3) snout-vent length—the distance from the tip of the snout to the anterior end of the cloacal orifice. Mittleman (1948) believed that sexual maturity was achieved at 38 mm in males and about 39 mm in females, his measurements being the conventional snout-vent distance (from tip of the snout to the posterior angle of the vent opening). However, such measurements, if valid at all for indicating sexual maturity, apply only to animals which metamorphose during the first year. Individuals from certain areas, i.e., Crater Lake, may require two years in the larval state and consequently reach a larger size before leaving water (Kezer and Farnner, 1955). These recently metamorphosed individuals commonly exceed 40 mm snout-vent length (*sensu* Mittleman) and yet retain gill stubs, a larval tail fin, lack a dorsal band and retain larval proportions. It appeared that a minimum snout-vent length of 48.5 mm would assure that the majority of the specimens were sexually mature and of adult proportions. It is of interest that Dr. James D. Anderson (personal communication) has recently pointed out that 48.5 mm is also the approximate size (average) of sexual maturity in *croceum*;

4) head width—maximum head width, usually just posterior to the eyes;

5) internarial distance—the distance between the medial margins of the external nares. This measurement was made with a calibrated eyepiece micrometer under a binocular dissecting microscope, each unit being equivalent to 0.083 mm;

6) interorbital distance—the distance between the anterior corners of the eyes, obtained in the same way as the internarial distance;

7) lens size—the greatest diameter of the extracted right eye lens, measured with the eyepiece micrometer, each unit equivalent to 0.023 mm. The lens has previously been used in salamander taxonomy by Hendrickson (1954) in studying the genus *Batrachoseps*;

8) total length—from the tip of the snout to the tip of the tail, taken with the animal on its back and flattened;

9) tail length—from the posterior margin of the cloacal orifice to the tip of the tail;

10) per cent of total length in tail—a ratio obtained by dividing the tail length by the total length;

11) axilla to groin distance—from the axilla or pit of the forearm to the groin, measured with the animal on its back and flattened;

12) span of hind legs—the distance from the tip of the longest toe of one hind foot to the tip of the longest toe on the other hind foot, measured with the animal on its back, the limbs at right angles to the body and adpressed to the table surface;

13) width of band—the widest portion of the band when rela-

tively unbroken, measured between the fore and hind legs at right angles to the body, or if broken into spots, the width of the widest spot. This measurement could not be obtained from many individuals of the race *macrodictylum*, their bands being too diffuse or indistinct to measure;

14) combined vomerine count—the number of teeth in the four series added together to obtain a single total count.

All subspecies, excepting *croceum*, were subjected to statistical analyses to determine if meristic differences could be correlated with geographic origin and pattern variation. For purpose of analysis, animals from each of the four races studied were pooled (*i.e.*, grouped) to form four samples. The several measurements tested were employed as ratios, a method used by Dunlap (1955) in working with frogs. Ratios were formed by dividing the larger number into the smaller. In one instance, per cent of total length in tail/ combined vomerine count, the two numbers varied as to which was larger. The vomerine count was usually the smaller figure.

The following fourteen ratios were tested: head length/ snout to vent; head length/ axilla-groin; head length/ per cent of total length in tail; head length/ length of right front leg; head width/ axilla-groin; head width/ snout to vent; head width/ head length; band width/ head width; band width/ interorbital distance; interorbital distance/ band width; interorbital distance/ axilla-groin; axilla-groin/ span of hind legs; length of right front leg/ axilla-groin; per cent of total length in tail/ combined vomerine count. In addition, the following ratios involving lens diameter were tested only between *columbianum* and *macrodictylum*: per cent of total length in tail/ lens diameter; axilla-groin/ lens diameter; span of hind legs/ lens diameter; snout to vent/ lens diameter; lens diameter/ total length. All ratios involving lens diameter were formed with the number of eyepiece micrometer units (usually a number between 50 and 100, each unit equivalent to 0.023 mm.) rather than the value obtained by conversion to millimeters. This procedure was suggested as a method of conserving digits by Dr. J. C. R. Li, biometrician at Oregon State College. Since only three digits beyond the decimal were saved in the formation of ratios, the number of micrometer units, being a large whole number, provided three useful digits. The converted millimeter value, being very small, provided only one or two useful digits beyond the decimal. Too few lens diameter measurements were available for *krausei* and *sigillatum*, these races being studied largely from borrowed material from which lenses were not usually removed.

The type of test used is based on the completely randomized Factorial Design and utilizes the Analysis of Variance based on the *F* distribution (Li, 1957). An equal number of males and females is used for each race, but the sample size for each race frequently differs. For every ratio three factors are tested: 1) race; 2) sex; 3) sex x race (interaction). A mean square value is calculated for

each of these factors, which when divided by the error mean square (pooled variance) yields an F value. The 1 per cent significance level is utilized in all tests.

The critical region is determined by the number of degrees of freedom, which ranges from 3 and 128 to 3 and 416 for race and sex \times race and from 1 and 128 to 1 and 416 for sex. The number of degrees of freedom depends upon the number of animals used in a particular test. Since the F values change only slightly between 120 and infinity, a value midway between that for 120 and infinity degrees of freedom was selected to establish the critical regions at $F > 3.85$ for race and race \times sex and $F > 6.75$ for sex. Since all of the calculated F values fall either well outside or inside the critical region, no case is disputable, and further refinement of the critical region is unnecessary. The critical region for all tests involving lens diameter (*columbianum* vs. *macrodictylum*) is $F > 6.75$ for race, sex and interaction.

When an F value for race exceeds 3.85 and is, therefore, significant, it indicates that the mean for the ratio being tested differs in two or more of the populations from which the samples were drawn and that such a difference would only be indicated in 1 of 100 times by chance. If an F value for race proves significant, the Individual Degree of Freedom is used to determine between which of the races the indicated difference is to be found. Thus, further F values are obtained by comparing *columbianum* \times *macrodictylum*, *columbianum* \times *krausei*, *columbianum* \times *sigillatum*, and *macrodictylum* \times *sigillatum*. These tests are also at the 1 per cent significance level, with the critical region being $F > 6.75$.

A significant F value for sex indicates that sexual dimorphism is exhibited in the ratio being tested. A significant F value for interaction (sex \times race) indicates that sexual dimorphism is not the same within one or more of the four races.

Table I gives the sample mean (M), the sample mean for each sex (\bar{M} , δM) and the number of specimens tested for each ratio. All F values obtained in the tests, the significant ones being indicated by an asterisk(*), are given in Table II.

STATISTICAL SUMMARY

Race.—The means of all 14 ratios tested for race were found to differ significantly. The source of variation is indicated in the following table:

Source of Variation	Differences (Significant F values)	Similarities (Non-signifi- cant F values)	Number Possible
<i>columbianum</i> \times <i>macrodictylum</i>	10	4	14
<i>columbianum</i> \times <i>krausei</i>	11	3	14
<i>columbianum</i> \times <i>sigillatum</i>	9	5	14
<i>macrodictylum</i> \times <i>sigillatum</i>	12	2	14

The means of five ratios involving lens diameter of *columbianum* and *macrodictylum* all were found to differ significantly.

The ratio head width/ head length is of particular interest for it was one which Mittleman claimed would differentiate his proposed subspecies. However, the present statistical data show that it fails to separate *krausei* and *columbianum* (*krausei* and *macrodactylum*, *sensu* Mittleman). Yet the ratio *does* separate *columbianum* from both *macrodactylum* and *sigillatum*, all three of which were included in the subspecies *macrodactylum* in Mittleman's treatment. The present statistical evidence clearly demonstrates many marked differences in comparisons made between *macrodactylum* and both

TABLE I.—Means and sample sizes for the samples treated in the statistical analyses

Ratio		Subspecies			
		<i>macro-</i> <i>dactylum</i>	<i>colum-</i> <i>bianum</i>	<i>sigil-</i> <i>latum</i>	<i>krausei</i>
Head length/ snout-vent	M	.219	.238	.239	.227
	♀ M	.217	.238	.238	.231
	♂ M	.221	.237	.239	.223
	N	160	126	100	38
Head length/ axilla-groin	M	.400	.454	.463	.431
	♀ M	.391	.449	.454	.429
	♂ M	.410	.459	.472	.433
	N	158	120	100	38
Head length/ per cent of total length in tail	M	.245	.284	.288	.249
	♀ M	.251	.298	.299	.263
	♂ M	.239	.270	.277	.235
	N	124	98	96	32
Head length/ length of right front leg	M	.801	.816	.803	.780
	♀ M	.855	.841	.832	.823
	♂ M	.747	.791	.775	.737
	N	156	120	100	38
Head width/ axilla-groin	M	.314	.345	.360	.329
	♀ M	.304	.336	.352	.315
	♂ M	.325	.353	.368	.343
	N	158	120	100	38
Head width/ snout-vent	M	.172	.180	.186	.173
	♀ M	.169	.177	.185	.170
	♂ M	.176	.183	.187	.177
	N	160	126	100	38
Head width/ head length	M	.788	.760	.779	.765
	♀ M	.779	.744	.776	.738
	♂ M	.797	.775	.783	.793
	N	160	126	100	38
Band width/ head width	M	.479	.496	.289	.405
	♀ M	.477	.509	.298	.405
	♂ M	.482	.483	.281	.405
	N	76	118	94	36

TABLE I.—(continued)

Band width/ interorbital distance	M	.754	.795	.460	.662	
	♀ M	.755	.815	.478	.698	
	♂ M	.754	.774	.441	.627	
	N		76	118	92	36
Internarial distance/ band width	M	.776	.755	1.345	.915	
	♀ M	.766	.734	1.312	.877	
	♂ M	.785	.775	1.378	.953	
	N		76	118	92	36
Interorbital distance/ axilla-groin	M	.195	.216	.229	.212	
	♀ M	.189	.211	.223	.204	
	♂ M	.202	.221	.236	.220	
	N		158	120	100	38
Axilla-groin/ span of hind legs	M	.760	.674	.655	.704	
	♀ M	.814	.692	.684	.753	
	♂ M	.706	.656	.626	.655	
	N		156	118	98	38
Length of right front leg/axilla- groin	M	.503	.559	.578	.551	
	♀ M	.458	.538	.547	.511	
	♂ M	.549	.581	.609	.591	
	N		156	118	100	38
Per cent of total length in tail/com- bined vomerine count	M	1.712	1.266	1.172	1.615	
	♀ M	1.595	1.212	1.147	1.484	
	♂ M	1.829	1.321	1.196	1.746	
	N		124	96	96	32
Per cent of total length in tail/lens diameter	M	.677	.538			
	♀ M	.658	.514			
	♂ M	.695	.561			
	N		88	44		
Axilla-groin/ lens diameter	M	.412	.338			
	♀ M	.424	.346			
	♂ M	.400	.331			
	N		114	44		
Snout-vent/ lens diameter	M	.750	.655			
	♀ M	.760	.664			
	♂ M	.741	.646			
	N		114	44		
Lens diameter/ total length	M	.654	.785			
	♀ M	.673	.791			
	♂ M	.635	.779			
	N		88	44		
Span of hind legs/ lens diameter	M	.538	.511			
	♀ M	.514	.503			
	♂ M	.562	.519			
	N		112	44		

TABLE II.—*F* values obtained in comparing sample means of ratios tested

RATIO:	SOURCE OF VARIATION										Total
	<i>F</i>	<i>DF</i>	Race	<i>columbianum</i> x <i>macrodactylum</i>	<i>columbianum</i> x <i>krasiei</i>	<i>columbianum</i> x <i>sigillatum</i>	<i>macrodactylum</i> x <i>sigillatum</i>	Sex	Sex x Race	Error	
Head length/ snout-vent	73.83*	3		156.90*	21.47*	.35	152.45*	.23 1	2.52 3	416	423
Head length/ axilla-groin	86.90*	3		164.03*	12.72*	3.77	201.58*	18.50* 1	.74 3	408	415
Head length/ T.L. in tail	91.01*	3		161.33*	57.86*	1.51	193.94*	70.01* 1	2.52 3	342	349
Head length/ Rt. F. Leg	4.86*	3		5.53	13.40*	3.13	4.97	220.08* 1	7.95* 3	406	413
Head width/ axilla-groin	71.14*	3		93.55*	10.77*	19.44*	191.40*	58.68* 1	.70 3	408	415
Head width/ snout-vent	50.09*	3		51.41*	17.16*	20.99*	131.76*	41.62* 1	14.71* 3	416	423
Head width/ head length	7.34*	3		20.17*	.34	7.66*	1.65	19.97* 1	2.25 3	416	423
Band width/ head width	95.53*	3		1.44	25.68*	250.11*	169.74*	1.53 1	.48 3	316	323

TABLE II.—(continued)

Band width/ interorbital distance	F DF	97.93* 3	3.41 1	21.99* 1	264.63* 1	164.98* 1	4.27 1	.52 3	314	321
Internarial/ band width	F DF	120.61* 3	.34 1	12.08* 1	307.37* 1	230.25* 1	3.03 1	.19 3	314	321
Interorbital/ axilla-groin	F DF	63.34* 3	93.75* 1	1.06 1	32.64* 1	232.47* 1	54.01* 1	.35 3	408	415
Axilla-groin/ Span hind legs	F DF	105.25* 3	139.00* 1	9.71* 1	7.34* 1	252.23* 1	217.09* 1	12.49* 3	402	409
L. Rt. F. Leg/ axilla-groin	F DF	77.03* 3	121.58* 1	1.06 1	10.71* 1	195.26* 1	289.70* 1	7.95* 3	404	411
1/2 T.L. in Tail/ T. Vomer. Count	F DF	50.41* 3	81.55* 1	22.14* 1	3.26 1	221.65* 1	15.14* 1	1.52 3	340	347
1/4 T.L. in Tail/ lens diameter	F DF		257.78* 1				24.43* 1	.31 1	128	131
Axilla-groin/ lens diameter	F DF		251.31* 1				26.51* 1	.90 1	154	157
Snout-vent/ lens diameter	F DF		157.37* 1				7.61* 1	.07 1	154	157
Lens diameter/ total length	F DF		142.20* 1				7.90* 1	1.33 1	128	131
Span H. Legs/ lens diameter	F DF		20.28* 1				52.84* 1	6.95* 1	152	155

* Indicates significance

sigillatum and *columbianum*. Although the two latter races differ in several respects, band width is the most reliable diagnostic characteristic. Whereas the ratios indicate *macrodictylum*, *sigillatum* and *columbianum* to be strongly differentiated, *krausei* is apparently the least strongly differentiated, especially as compared to *columbianum*, to which it must be most closely related. Yet, the morphological resemblance between *krausei* and *macrodictylum* is greater than that between *krausei* and *columbianum*, in spite of the fact that the ranges of *krausei* and *macrodictylum* are completely disjunct with *columbianum* occupying the considerable intervening area.

Sex.—Sexual dimorphism has been demonstrated in 10 of the ratios tested and is apparently due to the following measurements in all cases:

Axilla-groin	Females > Males
Per cent total length in tail	Males > Females
Length of right front leg	Males > Females
Head width	Males > Females
Interorbital distance	Males > Females
Span of hind legs	Males > Females
Lens diameter	Males > Females

Interaction (sex x race).—Interaction proved significant for five ratios, all of which is attributable to a more pronounced sexual dimorphism in *macrodictylum* and *krausei* compared to *columbianum* and *sigillatum*. A similar situation was noted with respect to sexual dimorphism of the vent.

KEY TO ADULTS OF THE SUBSPECIES OF *A. MACRODICTYLOM*

1. Dorsal stripe interrupted on the body, forming irregular but sharp edged spots; or band edges deeply undulated; band pigment of the head in small distinct dots or flecks. 2
- 1A. Dorsal stripe continuous on the body, with parallel edges (may be absent, diffuse or indistinct in *macrodictylum*); band on the head continuous to the snout, broken into well-defined spots or appearing as diffuse flecks. 3
2. Band color dull orange (Raw Sienna); ground color jet black; Santa Cruz County, California. *A. m. croceum*
- 2B. Band yellow; ground color brownish black; head wide, combined vomerine count exceeding 33; Douglas, Klamath and Jackson Counties, Oregon and the Sierra Nevada of California. *A. m. sigillatum*
3. Dorsal stripe continuous onto the snout, usually expanded on the head between the eyes and with a large patch on each eyelid; edges of the stripe nearly parallel; combined vomerine count less than 34; Montana, Alberta and E. British Columbia. *A. m. krausei*
- 3C. Dorsal stripe broken into spots or flecks on the head and snout; pigment on eyelids variable; edges of stripe diffuse, slightly undulated or parallel; vomerine count variable. 4
4. Band pigment of head, snout and eyelids in diffuse flecks; band often nearly absent, dull in color and tending to blend into the ground color; white flecks on the lateral body surfaces numerous and coalesced; vomerine count less than 34; head short and narrow; lens of eye small; Wil-

- lamette Valley of Oregon and W. of Cascade Mountains in Washington and SW. British Columbia. *A. m. macrodactylum*
- 4d. Band on the head, snout and eyelids forming large distinct spots; band bright in color and abruptly demarcated from the surrounding ground color; white flecks on the lateral body surfaces separate; vomerine count exceeding 33; head longer and wider; lens large; Cascades of Oregon, Washington, and British Columbia, east to the Bitterroot Mountains of Idaho; north through central British Columbia to S. Alaska.
 *A. m. columbianum*

LIFE HISTORY AND ECOLOGY

Breeding.—*A. macrodactylum* migrates to breeding ponds at various times of the year in different parts of its range. The time of migration apparently depends largely upon climate. In the Willamette Valley of Oregon, males begin arriving at the ponds in late October or early November, the females arriving shortly thereafter. The actual movement seems to coincide with the onset of the fall rains. The breeding season in this area is greatly prolonged, and the animals may remain in the pond or nearby vicinity until around the middle of April after which they disperse. Such a dispersal was noted at a small pond about six miles east of Corvallis on April 14, 1955 (the day was warm following a week of heavy rain). Prior to this date, adults could be found only under boards, leaves and other debris at the water's edge. However, at this time none was found at the edge of the water, but thirty-three were collected from under logs and boards located from 15-300 feet from the water.

In contrast to the breeding pattern west of the Cascades where the species is apparently active all winter, excepting for brief cold spells, a definite winter hibernation period is evident east of the Cascades. In this region of very low winter temperatures and heavy snowfall, the adults arrive at the ponds much later. Ferguson (1954) reports gravid females and eggs being collected at La Grande, Oregon on April 6, 1954. The actual migration to the ponds probably coincides with the melting of snow and warming weather.

On Vancouver Island near Langford Station, 8 miles northwest of Victoria, Carl (1942) reports finding freshly spawned eggs on March 9, 1941. Fitch (1936) found freshly spawned eggs in mid-February and mid-March in the Rogue River Basin in Oregon. Bishop (1947) collected eggs and adults in ice-bordered ponds at Reflection Lakes on the slopes of Mt. Rainier, Washington on June 25, 1936. Kezer and Farner (1955) believed the eggs to be deposited in the vicinity of Crater Lake in May, June and July, depending upon the location and type of pond. Hatching eggs were reported at Mollman Lake (elevation 7,130 feet) in the Mission Mountains of Montana on August 3, 1950 by Brunson and Demaree (1951).

The total number of breeding individuals using a particular pond was found to be quite large by Storm and Pimentel (1954) who carried on marking and trapping studies near Corvallis, Oregon.

They report up to 394 individuals using a pond of one-seventh acre extent.

The number of eggs laid by the female is quite variable. Slater (1936) records taking 184 mature eggs from a female measuring 127 mm in total length. Below are listed the numbers found for several females from several localities in the present study. The date of collection indicates in a general way the breeding season for the area involved.

Locality	Total Length	Snout-Vent	No. Mature Eggs	Date Collected
Near Corvallis, Linn Co., Oregon	102.2	54.7	158	1/16/55
Corvallis, Benton Co., Oregon	133.0	68.0	199	1/1/54
Near Corvallis, Linn Co., Oregon	97.7	55.0	219	11/19/55
Near Corvallis, Linn Co., Oregon	107.3	60.7	208	11/19/55
Near Corvallis, Linn Co., Oregon	109.0	57.6	179	11/19/55
Near Corvallis, Linn Co., Oregon	104.5	58.0	130	11/19/55
Near Keno, Klamath Co., Oregon	132.0	70.5	345	4/4/56
Near Medford, Jackson Co., Oregon	105.6	58.6	198	3/20/55
La Grande, Union Co., Oregon	98.0	52.7	85	4/24/54
La Grande, Union Co., Oregon	71.0	87	4/20/54
Moscow, Latah Co., Idaho	119.7	61.9	145	4/13/54

The eggs may be found singly but are more frequently in plinths, attached to the stem of an aquatic plant, rock or other object. Gravid females deposit masses of eggs on toweling when kept in the laboratory in large glass containers. A single mass may contain from 5-25 eggs but average 10-12 per mass. Slater (1936) described the ovum as 2.5 mm in diameter, black at the animal pole with the lower 2/5 at the vegetal pole being grey; two jelly envelopes are present with the line of demarcation between being indistinct; inner envelope 6-7 mm in diameter, outer 12-17 mm depending upon the age of the egg.

Larval Development.—Kezer and Farner (1955) found three rather clearly defined life history patterns for *A. macrodactylum* in the vicinity of Crater Lake: 1) One season larval period, where the

eggs are deposited in the spring, and the larvae transform in late August or early September. This appears to be the "normal" course of events. 2) Two season (or more) larval period wherein the larvae do not metamorphose the first year but over-winter and do so the following year, attaining a length of 70-90 mm at the time of transformation. 3) Facultative one season larval period wherein the larvae are forced to metamorphose by the drying of a semipermanent pond. These larvae form very tiny transformed individuals.

Similar patterns are probably found throughout the ranges of *sigillatum*, *columbianum* and *krausei*, the type of pond and elevation determining the one present in a given area, with seasonal variations caused by macroclimate. Evidence is lacking that *A. m. macrodactylum* ever has a two-year larval period. Young *krausei* from Kootenai Crossing, British Columbia examined by me fall into two definite size classes, representing some animals of the two-year larval type (large gill scars, a faint band and a line or seam present down the dorsal midline representing the vestiges of the tail fin) and some which metamorphosed the first year (small, adult pattern and no gill scars evident). Recently metamorphosed *columbianum* from several localities in Deschutes County, Oregon appear to belong to the two-year larval class. Stebbins (1951) mentions larvae of two distinct sizes reported by H. J. Snook in Alpine County, California. Dr. James D. Anderson (personal communication) reports all three life history patterns in Sierra Nevada populations, but states that the distinction between 1 and 3 (above) is not always clear.

Dr. R. B. Brunson of Montana State University (personal communication) has called to my attention the very small size of newly metamorphosed young in western Montana, where the facultative pattern is apparently common. The smallest metamorphosed individual examined was from that area.

Habitat.—Ecologically and geographically, *Ambystoma macrodactylum* is one of the most adaptable and variable salamanders in the Northwest, surpassing all other species in these respects. Confirmation of this fact is evident in the range of the species, which includes sagebrush semi-desert and all the intermediate vegetative types up to alpine meadows.

In the Willamette Valley *macrodactylum* is found in bottom land situations or in oak woodlands along the valley edges, where it breeds in permanent and semi-permanent ponds. Although the animal is easily found near such ponds during the breeding season, it is exceedingly difficult to locate at other times. It apparently leads a subterranean existence during the dry season, probably residing in rodent burrows and other underground excavations. Although it is repeatedly depicted as being found on the Oregon coast, the species does not appear to occur in the coastal type forests surrounding the valley. Moreover, only two records are available from the coast, one on the Rogue River and Baird's record from near Astoria, both of

which are located on large rivers draining inland areas where the animal commonly occurs. It is questionable whether the species inhabits other coastal areas not drained by large streams transecting the Oregon Coast Ranges.

Of the four subspecies treated here, *columbianum* is probably least restricted as to habitat distribution. It has been recorded from 7,800 feet (Hudsonian Life Zone) in the Wallowa Mountains of northeastern Oregon (Ferguson, 1952b) where the vegetation consists of stunted willow (*Salix sp.*), limber pine (*Pinus flexilis*), and various grasses and sedges. Less than 40 miles from this locality, the animal has been found occupying an abandoned mine shaft at a place about 10.3 miles north of Home in the Snake River Canyon of Baker Co., Oregon by Ferguson, *et al.* (1958). This locality is Upper Sonoran Life Zone (elevation roughly 1,800 feet), the vegetation being primarily a sparse cover of sagebrush (*Artemisia tridentata*), cheat grass (*Bromus tectorum*) and scattered hackberry trees (*Celtis douglasii*). Ferguson (1952a) reported adults being difficult to locate during the summer but larvae abundant in springs and ponds throughout the yellow pine forested areas of Wallowa County, Oregon.

Fitch (1936) found *sigillatum* to occur irrespective of life zone from Crater Lake down to less than 2,000 feet in the Rogue River Valley, a fact further indicated in the present study by collections made near Medford (1,150 feet) and Crater Lake (6,170 feet). Fitch believed the adults to be subterranean in habit during the dry seasons in the Rogue River Valley. However, at Crater Lake, Farner and Kezer (1953) were able to obtain adults throughout the summer along the edge of the lake. Stebbins (1951) mentions records from 6,820 and 7,000 feet elevation in Alpine County, California. Also, Anderson (personal communication) has found them a few feet shy of 9,000 feet in Alpine County.

A wide variety of habitats and elevations are also occupied by *krausei*. Brunson and Demaree (1951) report it at 7,130 feet in the Mission Mountains. Several records are available from the Bitterroot Valley near Missoula. Specimens of *krausei* were obtained July 15, 1955 near John's Lake, Glacier National Park, Montana (elev. ca. 3,500 ft.) from an unusual habitat. In working around the lake, although all likely looking logs, sticks and other objects were turned and a thorough search made for salamanders, only a single recently metamorphosed animal was found. However, just before giving up, a fallen log was torn open and a salamander was found. Continued search yielded five other animals in rotting hemlock (*Tsuga heterophylla*) logs, most of which were located 25-100 yards from the water. The lake is surrounded by a rather dense forest of spruce (*Picea engelmanni*), western red cedar (*Thuja plicata*), hemlock and scattered maple (*Acer sp.*), resembling the type of forest found in parts of western Oregon. The niche was similar to that occupied by the salamander *Aneides ferreus* in western Oregon, where it fre-

quently occurs abundantly in rotting Douglas fir logs (*Pseudotsuga menziesii*).

Russell and Anderson (1956) described the habitat of *croceum* in considerable detail. Briefly it is predominantly oak forest (*Quercus agrifolia*), with Madrone (*Arbutus menziesii*) and Douglas fir (*Pseudotsuga menziesii*) sparingly represented.

When *columbianum* from Union Co., Ore., *sigillatum* from Jackson Co., Ore. and *macrodictylum* from Benton Co., Ore. were placed in finger bowls with moist toweling, the *macrodictylum* sought refuge beneath the toweling, the others being content to remain exposed. This was interpreted to indicate a lesser ability in *macrodictylum* to cope with drying. Preliminary dehydration tests, in which *macrodictylum* lost an average of 33.5 per cent of their original body weight compared to 28 per cent loss in *columbianum*, appeared to substantiate the hypothesis. However, small samples were used and the studies were discontinued when additional living specimens could not be obtained simultaneously from the two areas due to seasonal variation in availability.

Notes on Food, Enemies and Size.—Detailed studies were not made of food habits, this aspect having been investigated by Farner (1947) and Schonberger (1945) at Crater Lake. Their work indicates the species to be primarily scavengers, feeding largely on insects and insect parts. Farner found *A. m. sigillatum* not to feed on snails, whereas *Taricha*, which frequently occurred under the same rock, did do so. However, in the present study, two types of snail shells were abundant in the fecal pellets of several *A. m. krausei* from Eisenhower Forks, Alberta, Canada.

Regarding enemies, adults probably do not often fall prey, they being so secretive at times other than the breeding season. However, two adults in the University of California Collection (MVZ 24707 and 24698) were removed from the gut of a garter snake (*Thamnophis*) collected in Creighton Valley, British Columbia. Larvae are probably devoured in quantity by predaceous aquatic insects and garter snakes. On April 10, 1956 near Corvallis, Oregon two *Thamnophis sirtalis concinnus* were observed actively foraging in a shallow pond containing large numbers of *A. macrodictylum* larvae.

The largest *A. macrodictylum* examined was a female *columbianum* in the College of Puget Sound Collection (CPS 3011) from 21.3 mi. NE Goldendale, Klickitat Co., Washington. Measurements (after preservation) were 155.6 mm in total length (167 mm in life) and 79.6 mm snout-vent. This exceeds the largest previously known specimen from Wallowa Co., Oregon which measured 155 mm before preservation (Ferguson, 1952b). A preserved male from near Philomath, Benton Co., Oregon measured 151.3 mm in total length and 74.0 mm snout-vent. Two specimens from Plumas Co., California approach these maximum figures.

The smallest transformed animal examined was a specimen from John's Lake, Glacier National Park, Montana (DEF 606, now in the Park Collection), which measured 43 mm in total length and 29 mm snout-vent.

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Social Behavior of the Desert Pupfish, *Cyprinodon macularius*, in the Field and in the Aquarium

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ABSTRACT: A glossary of the motor patterns of the desert pupfish is given. Reproductive, territorial and group behavior is analyzed in detail. During the breeding season the female visits the territorial male; rarely, males leave their territories and pursue the females in order to spawn with them. When approached by the male, the female nips the bottom, the male sidles against her, she halts and forms an S-shape, the male S-shapes along side the female and wraps his anal fin around her vent, she jerks releasing an egg, the male jerks fertilizing the egg, and the pair separates.

In a fully developed fight two males approach head on, turn away slightly and stand momentarily eye to eye, advance and arch, give tail-beats, charge at one another, and finally circle head to tail rapidly around one another before separating.

During the spawning season males hold territories, and these sometimes contain sub-territories along the periphery which are held by smaller males. Females were never seen to hold territories under natural conditions.

Female and juvenile pupfish move about in schools and forage in groups. In the cold season the males join the schools.

INTRODUCTION

The interpretation of animal phylogeny through the comparative study of species-specific behavior patterns started with the independent works of Whitman (1899, 1919) and Heinroth (1911). It was not until the recent writings of Lorenz (1939 in Schiller, 1957) and of Tinbergen (1940, 1951) that this approach to the study of behavior gained impetus. So far the rewards have been exciting but limited; in most animal groups the total body of information is still too small (see review by Eibl-Eibesfeldt and Kramer, 1958).

An excellent example of a numerous and well known group of animals whose ethology is virtually unknown are the teleost fishes of the family Cyprinodontidae, the toothcarps. A brief ethogram of the breeding behavior of *Oryzias latipes* (Temminck and Schlegel) has been published by Ono and Uematsu (1957), and a short account of the behavior of *Fundulus notatus* (Rafinesque) has been given by Carranza and Winn (1954), and that of *Fundulus diaphanus* (Le Sueur) by Richardson (1939); Koster (1948) has published a note on the spawning activities of a closely related species, *Plancterus kansae* (Garman). Peters (1941) has presented a condensed description of the social behavior of *Jordanella floridae* Goode and Bean. Newman (1907), and Raney *et al.* (1953), have reported on some aspects of the behavior of *Cyprinodon variegatus* Lacépède. The article by Raney *et al.* (1953) also cites incidental observations from

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the literature on different species of *Cyprinodon*. Within recent years aquarists have photographed the behavior of fishes with the aid of electronic flash equipment; the articles in various aquarium journals by Foersch in particular are of use in the comparative study of tooth-carp because of the excellent photographs.

It is the purpose of this paper to describe the motor patterns and social behavior of the desert pupfish, *Cyprinodon macularius* Baird and Girard. The reader should appreciate that this short paper can only be an introduction to the ethology of the desert pupfish.

I am indebted to Donald K. Adams, Boyd W. Walker, and Wolfgang Wickler for critically reading the manuscript. Thanks are also due to John Wintersteen for filming the spawning behavior of the desert pupfish and to Herman Kacher for preparing the illustrations. Clark Hubbs kindly made available certain of his field notes on the behavior of other species of *Cyprinodon*.

MATERIALS AND METHODS

Adults of both sexes of the pupfish often attain a standard length of 45 mm. One exceptionally large female 72 mm in length was collected. Sexual maturity may occur in males as small as 15 mm long, and the same probably holds for females.

When mature the sexes are distinctly dimorphic and dichromatic. The body shape of the male is compressed and arched at the nape, whereas the shape of the female is rounded (Fig. 1A). In the breeding season the body, and the dorsal and anal fins of the male are dark metallic blue; the caudal peduncle, caudal fin, and pectoral fins are yellow-orange. The eyes are black, and so are the posterior margins of the dorsal and anal fins. The lower distal portions of the pectoral fins are much darker than the other parts of the fins. When the water is clear these males can be seen at distances up to 10 meters. The head and body of the female are yellowish brown with irregular darker brown blotches; the fins are similarly colored. During the spawning act the body is paler and an interrupted brown line extending mid-laterally the length of the body becomes more apparent. Except for the small dark ocellus found at the posterior base of the dorsal fin in the female, the juvenile and female markings are the same. The colors of the female and of the juvenile pupfish render the fish inconspicuous because they correspond to those of the algal mats which coat the bottoms of the desert pools that are their habitat.

The desert pupfish is widely distributed in the desert springs and drainages of the lower part of the Colorado River Basin (Miller, 1943). In the Salton Sea the pupfish occurs in shallow shore pools where they are easily observed. This habitat, and some aspects of the ecology of the pupfish therein, have been described elsewhere (Cowles, 1934; Barlow, 1958). More general information on the ecology and life history of the desert pupfish can be found in Miller (1943, 1949).

Almost all of the observations from the field were on pupfish living in shore pools along the Salton Sea. Supplemental observations were made at nearby Fish Springs. The shore pools were visited at about monthly intervals over a two year period from 1954 to 1956. Most observations were made in the forenoon although the fish were also watched at other times of the day as well as during the night.

Pupfish of mixed sexes and sizes were also maintained in a freshwater aquarium, having a capacity of 68 liters, which was well planted. Previously isolated males and females were put together in 45 liter aquaria which contained no plants; the bottoms were covered with fine gravel. This experiment was repeated four times, and in each instance the female was the resident fish. An additional pairing was filmed in color at normal and at high speeds. The film proved especially useful in the descriptions of the motor patterns.

MOTOR PATTERNS

The characteristic movements which constitute the behavioral repertory of the pupfish have been given names to facilitate discussion. Convenience has been the rule in deciding which complex of motor patterns should be considered as units. Thus *patrolling*, which actually consists of several motor patterns, is treated as one element. The individual movements, however, are described. On the other hand, *wrapping* seems to represent a single motor pattern, and it is described as another unit in the behavior on a par with *patrolling*.

Meandering.—The female swims slowly in midwater or near the surface, changing course frequently and rather aimlessly. Swimming movements seem to be slightly exaggerated. The median fins are held against the body.

Nuzzling.—The male swims directly under the female while she meanders. His body is tilted up about 30° , and he maintains a position in which the top of his head is just below, or in contact with, the abdominal region of the female (Fig. 1D). (The abdominal region here includes the ventral surface from directly below the pectoral fins to just posterior to the vent.) The median fins of the male are folded.

Contacting.—As the female moves slowly over the bottom the male stays beside her, and her head is usually just in front of his. Often they are actually touching. In the early stages of the mating the male usually contacts the female anteriorly in the region of her pectoral fin base with his snout. As mating proceeds, the male contacts the female progressively more posteriorly. Eventually, the area of contact is almost restricted to the region of the vent. During most of this time the dorsal fin is folded. Movements of the male which are directed at keeping station beside the female are called *contacting*. Side to side contacts are not separated from snout to side contacts.

Tilting.—While swimming slowly over the bottom the female tilts her body toward the bottom, head down, at an angle of about

45°. The dorsal fin is normally raised at this time. Tilting is the beginning movement of nipping.

Nipping.—From the tilted position, the female opens her mouth, presses it against the bottom, and normally takes up a mouthful of the substrate (Fig. 1B). Then the body is dropped down against the bottom. When horizontal, the female either immediately spits out the substrate, or swims forward a short distance, stops, and then expels it. The female appears to turn the substrate over in her mouth. The dorsal fin is held open. The female may nip two or three times in quick succession; each successive nip after the first one is initiated from the horizontal position. Females of another toothcarp, *Cyprinodon variegatus*, were seen by Raney *et al.* (1953) to pick up objects from the bottom when encountered by males, and this action was interpreted as food-seeking. In the roach, *Leuciscus rutilus* (L.), and in the goldfish, *Carassius auratus* (L.), the female evidently signals the moment of spawning by snapping at some object as if feeding (Fabricius, 1959).

Halting.—The female stops swimming after nipping. Usually her vent is close to the substrate so that the long axis of the body is tilted up slightly anteriorly (the male assumes a corresponding angle). The dorsal fin is still spread.

Sidling.—The male swims forward and laterally against the female. The male's dorsal fin is folded or half open. The region supporting the anal fin of the male is thrust against the posterior line of the abdomen of the female. The body of the male is tipped out of the median plane only slightly, or not at all. In this maneuver the male cannot swim by means of trunk undulations and must therefore rely on sculling movements of the free pectoral fins and of the caudal fin. This rapid sculling imparts a quivering appearance to the male.

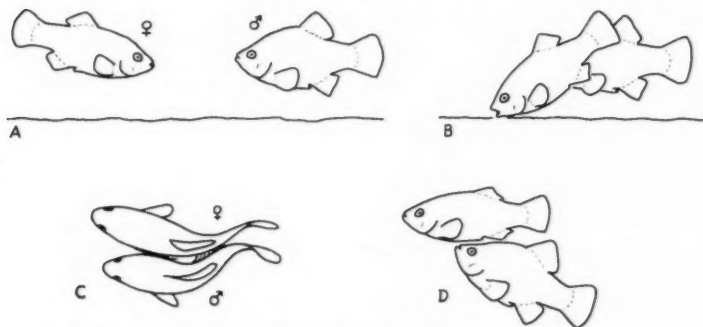


Fig. 1.—Motor patterns of the desert pupfish. A. A male approaching a female. Note the rounder profile of the male. B. The female just about to nip while being contacted by the male. C. The male and female S-shaping; the male is also wrapping. D. The male, below, nuzzles a meandering female.

S-shaping.—Seen from above, the body of the pupfish forms a gentle "S" (Fig. 1C). At this time the male and female normally lie side by side on the bottom in parallel S-shapes. The curvature is more pronounced in the male. The head and the anal region of the male are directed toward the female, and the anal fin of the male is extended in her direction. The dorsal fin of the male is spread, and sometimes is bent slightly toward the female. In the female the dorsal fin is spread maximally. Moreover, her vent is pressed against the bottom and her caudal fin beats rapidly, but with a very small amplitude.

Wrapping.—While both fish are S-shaped the male wraps his anal fin around the posterior line of the female's belly (Fig. 1C). The male's anal fin forms a crude cup under the vent of the female. The extended dorsal fin was sometimes bent toward the female, but it was never seen to enfold her.

Jerking.—While still S-shaped the head is jerked toward the side opposite that to which it is already directed, thus initiating a wave of contraction which passes down the body reversing the direction of the S-shape. In the female one egg is extruded by this flexure, and the male presumably emits sperm at this moment.

Patrolling.—The male in his territory swims straight ahead in spurts of about 30 to 50 cm with the dorsal, anal and pectoral fins folded back. The lateral beats of the orange caudal fin contrast against the bright blue body. At the end of each spurt the male stops abruptly by throwing the colorful pectoral fins forward together in a quick movement that catches the eye. Then the male stands momentarily with the median fins raised, and the pectoral fins beating alternately and rapidly. The caudal peduncle is frequently flexed to one side in the intention swim posture. Then he swims off again in a new direction. In this manner the male pupfish continually crisscrosses his territory.

Facing.—Males approach one another head on and usually pause momentarily face to face about one body length apart. The median fins are spread.

Eyeing.—Two male stand momentarily eye to eye facing in opposite directions, bodies parallel, and about one half body length separating them. The median fins are spread.

Arching.—The body is bent into a C-shape with the concave side toward the other fish. The median fins are spread. A sculling action of the caudal fin and the pectoral fin on the convex side imparts a slight quivering appearance to the fish.

Tail-beating.—The flexure of the peduncle appears to be reversed from the arched position so that the caudal fin, apparently folded, is first directed away from the other fish. Then the spread caudal fin is beaten back toward the opponent, often causing the

head of the fish delivering the beat to swing away. This movement requires further observation.

Charging.—The median fins are folded, the mouth is opened, and the fish darts forward toward another fish.

Circling.—From the arched position two fish often start to circle at high speed while maintaining the head to tail orientation. It seems that each fish attempts simultaneously to charge into the flank of the other and to dodge the charge of the opponent by turning.

Fleeing.—The fish swims away from the attacking fish at high speed with the median fins folded. Flight is toward the surface in the absence of cover, but if plants are present the fish will sometimes take refuge among them.

Escaping.—The fish darts toward the bottom and into the mulch, algae, or plants there, and then lies motionless. Cowles (1934) observed this behavior in free living pupfish which he tried to capture.

Digging.—While standing over the bottom, with head and body tilted downward about 45° , the fish moves ahead, *i.e.*, obliquely downward while opening the mouth. The mouth contacts the bottom; substrate is taken into the mouth; the fish rebounds; the body is tilted up into the normal horizontal position as the fish moves forward slightly; and the substrate is expelled through the mouth. The substrate is often expelled immediately at the end of the rebound.

Plowing.—This movement starts just like digging, but when the substrate is taken into the mouth, the fish then drops the body down against the bottom and swims forward through vigorous beating of the tail. At the same time, the pectoral fins beat forward resisting the thrust of the caudal fin. The fish briefly swims in place expelling bottom material both forward and backward. Then the pectoral fins cease to resist the tail propulsion, and the fish moves forward expelling the mouthful of substrate. After this the pupfish commonly returns to the excavated spot and digs there in the normal manner. According to the description by Raney *et al.* (1953), *Cyprinodon variegatus* plows in the same way. Plowing in *Cyprinodon* seems similar to the movements in cichlid fishes which have been called digging by Baerends and Baerends-van Roon (1950).

REPRODUCTIVE BEHAVIOR

The behavioral acts in the reproduction of the pupfish proceed in a characteristic sequence. The sequence of events described in the following represents a composite of four series of observations on different pairs of pupfish in aquaria.

When a male is introduced into the aquarium he sinks to the bottom where he remains motionless. His colors fade slightly, apparently due to the handling. The female immediately fixes on the male and moves toward him. This is followed by aggressive behavior by the female. She starts by arching while facing the male.

The tail of the female is brought around and directed toward the male. Then she backs in the direction of the male while maintaining the arched position. When her tail is near the head of the male she commences tail-beating. The blows are directed at the head of the male. The male responds by fleeing, normally toward the surface, or less often by arching and returning tail-beats. In the latter case the two fish may charge at one another leading into circling head to tail. This is typical fighting as seen between two males.

The aggressive activity of the female is sporadic. After a variable period both fish become inactive, and the colors of the male return. They lie on the bottom about two to three body lengths apart and facing one another. The attention of the female is fixed on the male. Five to twenty minutes after his introduction into the aquarium the female suddenly nips the bottom. At once the male swims to her side and contacts her. She swims forward over the bottom with the male maintaining contact. The female tilts about every 3 to 5 seconds, and some of these movements develop into complete nipping. The male drops back slightly after each nip by the female and attempts to sidle. At first this seldom develops into wrapping because the female does not halt completely. Each nip-to-sidle sequence brings the pair a little closer to complete spawning. At about the third to fifth nip by the female the male usually succeeds in wrapping because the female now halts completely. Sidling by the male apparently releases S-shaping by the female, which in turn causes the male to S-shape, and almost concurrently, to wrap the anal fin around the vent of the female. Wrapping then releases jerking in the female, which is almost simultaneously followed by jerking in the male. The pair separate and one egg is left on the bottom. Rarely, the female immediately S-shapes and the sequence proceeds through to jerking again without the pair separating. Successive jerks indicate that up to five eggs may be spawned in quick succession. Normally the pair moves forward a short distance between successive jerks. Sometimes when they separate the female swims up into midwater and meanders. The male accompanies her and continuously nuzzles her.

The spawning lasts from 30 minutes to 2 hours, larger females spawning longer than smaller. Usually the last union of the pair is the most prolonged, and several eggs are released in quick succession, then both fish lie still on the bottom. After about 2 seconds the male starts contacting the female again. If the female is through with spawning she darts toward the surface. The male pursues and the female seems "panicky," sometimes breaking the surface. This rapid and evasive swimming by the female contrasts sharply to meandering. After about 5 minutes the male stops chasing the female. Both swim to the bottom and without further interaction start foraging.

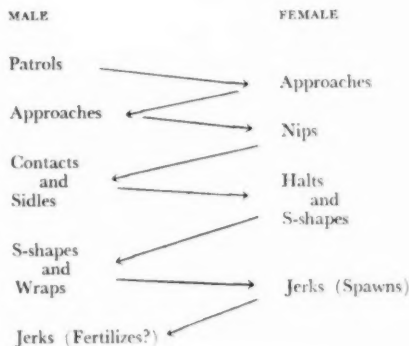
Most of the variations observed could be considered under one or the other of two categories. The first is orientation. In the initial

stages of spawning one male contacted the female at first in the region of the pectoral fin, and later only near the vent; another male contacted first and only near the vent. Abortive contact resulted when a male once contacted a female who was about 5 cm over the bottom of the aquarium. Later this male attempted, without success, to contact the female while facing the opposite direction, i.e., situated head to tail. One female oriented her spawning activities to the bottom in the normal fashion during the first half hour of spawning, but in the next 20 minutes she oriented to one glass wall as though it were the bottom. She stayed parallel and adjacent to the water surface with her ventral surface against the glass wall. She nipped the glass though no gravel was present. The male did not contact until the female assumed the S-shape. Then the male oriented to the female, not the substrate, and the pair spawned.

Another source of variation lies in the sequence of movements. This type of variation is most obvious at the beginning of pairing. Usually one fish appears at first more inclined to spawn than the other. For example, one female invited the male to spawn by nipping, but when the male contacted her, she responded by arching and tail-beating. During 3 to 4 more contacts by the male the behavior of the female gradually became synchronized with that of the male, and spawning proceeded following the typical sequence.

Even when the pair finally is synchronized the sequences varies, but the variation is not random. In the behavioral sequence shown by the male from approaching to wrapping, for instance, if the female is not ready to halt, the male may stop sidling or wrapping and revert to contacting. Where he starts again depends on the behavior of the female. If she moves away the male may revert to contacting. But if the female resumes S-shaping, then the male also starts at S-shaping. Thus elements in the sequence also may be omitted. At the peak of spawning, about one out of every four contacts proceeds to jerking. Ultimately the variation in sequence is due to the variation in the physiology of the two fish. For example, a female whose threshold for releasing an egg is presumed to be low, stays in place when she nips, but when the threshold is presumably somewhat higher, she moves forward as much as two body lengths before halting. At an apparently higher threshold she may tilt without nipping. And this determines the response by the male.

The sequential nature of the reproductive reaction chain is given in the



style of Tinbergen (1942). This diagram applies to naturally occurring populations, not to pupfish in aquaria, and represents an "ideal" stimulus-response chain.

Some elements of the behavior of the pupfish seen in aquaria were lacking or uncommon in the natural population. No female was seen to meander although once a male was observed nuzzling a female which was lying just under the water surface. Contacting infrequently was seen as a behavioral unit separate from sidling.

Two different types of reproductive behavior were observed in the field. In the typical situation the male remains in his territory and the females, alone or in groups, visit him there. If the female is alone it is almost certain that a spawning will occur at once. Usually only one egg is laid, they separate, and the female swims away. If a group of females enters the territory, the male swims directly to the nearest one and pauses. He swims from one female to the next until one gives the proper response. The females without eggs forage continuously. When the male encounters a female who is ready to spawn, she nips, the male immediately sidles, and the sequence runs through to jerking. Then they separate, the male resumes patrolling, and the females move on, alternately schooling and foraging. Rarely the male from a neighboring territory rushes to the side of the female opposite the first male, and spawns with the pair. Raney *et al.* (1953) reported that in *Cyprinodon variegatus* two males sometimes spawn together with one female.

A kind of reproductive behavior seen less frequently occurs when 1 to 3 males pursue a given female over considerable distances without regard to territorial boundaries. The female does not meander, but swims rapidly. Every 1 to 3 meters the fish stop on the bottom and spawn. On one occasion a group of 3 males and 1 female remained still on the bottom for about 4 seconds after spawning. The spawning groups never stopped in the occupied territory of another male. I was unable to determine whether or not males spawning outside territories themselves held territories. *Cyprinodon variegatus* also shows both of these types of reproductive behavior (Raney *et al.*, 1953).

Two chance observations are worth noting because of their relevance to the problem of sex recognition in pupfish. A group of males were held together in a small tank with a capacity of about 30 liters. One large male quickly became dominant. He continuously pursued the smaller males. Finally one fish was so exhausted by the dominant male that it could no longer flee. Then the large male sidled against the smaller, S-shaped, wrapped, and jerked. This behavior was repeated many times within an hour. On another occasion 3 previously isolated females were placed in a beaker. About one-half hour later a brightly colored male was put into the same beaker. The male sank to the glass bottom, faded slightly, and remained motionless. One of the females swam directly to him, pressed herself against him, S-shaped, and jerked. The male did not respond.

AGGRESSIVE BEHAVIOR

The size of the opponent appears to determine the first response of a territorial male. If the other pupfish is a smaller male (but not too small, see p. 352), usually the first move of the larger fish is to charge straight at the opponent, who generally flees. If the opponent is at least as large, or larger, the two commonly face one another, and then in rapid sequence eye one another, arch, give tail-beats, and finally charge and circle. At this point the fight normally breaks off. If one flees, the other may pursue. Evenly matched males commonly swim away from one another after circling; however, they may stand about one body length apart, arch, and give emphatic tail-beats. This can lead into charging and circling again.

Fighting can be observed among both male and female *C. macularius* throughout the year in a well-lighted and warm aquarium. Males, however, fight more than females. The fighting in females is rarely carried to circling. In addition, males attack females when the males are not ready to spawn, as Cowles (1934) has noted.

Fighting among pupfish in the desert pools is similar to that observed in aquaria. Noteworthy variations and comparisons, such as whether or not a male attacks females, or smaller males, will be considered in the description of territoriality.

TERRITORIALITY

The males of different species of *Cyprinodon* are well known for their pugnacious defense of territories (Newman, 1907; Cowley, 1934; Raney *et al.*, 1953). When placed in a new aquarium, males of *C. macularius* fight considerably until territorial boundaries are established. After this the amount of fighting is reduced and restricted to the boundaries; each male stops there, arches as the neighboring male approaches and then each swims back toward the center of his territory. Rarely one charges at the other and then both circle quickly and depart. Intruders that stray into a territory, at first unnoticed by the resident, elicit a head-on charge by the latter when he finally discovers them. The intruder almost always flees. Fish without territories flee into thickets of plants, or toward the surface.

Due to the spatial limitations imposed by the aquaria, the territories established in them were comparable in size only to the smallest seen in natural pools. The maximum number of territory holding males in a tank with a bottom measuring 30 cm by 60 cm was 4, varying in standard length from 25 mm to 30 mm. Moreover, it is almost impossible to induce only 2 males to maintain territories in the same aquarium. Invariably one supplants the other and dominates the entire bottom.

The presence of food determines the territorial center of the largest male. It is possible to shift the territory of the largest male as desired by gradually changing the place where the food is put into the aquarium.

Females defend territories only when the number of fish in the tank is small, and this behavior is rather sporadic. But when aggressive, females will sometimes defend territories in aquaria even against smaller males. Where several females are together the larger and stronger ones defend the center of the feeding area at feeding time. Otherwise a rank order is maintained, though this has not been observed in detail.

Male pupfish in the shore pools defend certain areas during much of the year. The consistent holding of territories extends from mid-April, or May, to October. During periods of warm sunny weather in the winter males sometimes come into nuptial coloration and take up territories, as was observed on 11 February 1956. The females were never seen to hold territories. However, Raney *et al.* (1953) reported one instance of a female *Cyprinodon variegatus* briefly maintaining a territory in a pool against other females.

The holding of territories in the pools seems to fluctuate during the day, but this requires further observations. Large males were seen now and then to leave their territories late in the afternoon to forage in shallower regions of the pools although they forage within their territories as well. Raney *et al.* (1953) noted that *C. variegatus* males also stray from their territories. At night most territorial males of *C. macularius* sleep in their territories, whereas the non-territorial pupfish sleep in the shallowest possible water. At sunrise territorial and non-territorial fish alike congregate in the deepest parts of the pools (Barlow, 1958).

Male pupfish maintain territories in different parts of the pools, and certain features seem to characterize these territories. First, they are never located in deeper (one meter) parts of the pools. A typical situation is one where territories are located in water about 5 to 10 cm deep and along the edge of a drop-off into deeper water. Secondly, marked irregularities in the topography of the bottom are usually present. Territories are centered about such objects as submerged bushes, pieces of wood lying on the bottom, corners or coves along the shore, or outstanding features of the bottom profile. This is especially clear where large areas of the bottom are flat. There, at the peak of the breeding season, nearly every piece of debris is patrolled by a brightly colored male.

The male pupfish recognizes his territory by several features of the terrain. One male was seen patrolling up and down a sunken palm frond. The frond, about one meter long, lay flat on the bottom, half in and half out of a tiny cove, and extended away from the shore at a right angle. The cove was semicircular in shape with a radius of about 50 cm. The territory of the male included the cove and extended out into the pool along the frond. I moved the frond so that only one third of its length remained in the cove. The male returned to the cove shortly, swam to the frond, and resumed patrolling along it. Then I moved the frond so that it lay just outside of the cove. Again the male returned first to the cove, but then patrolled along

the frond. Finally, I moved the frond about one meter away from the cove (for each move the water depth remained approximately the same). As before, the male went to the cove and from there to the frond. However, after the male swam up and down the frond once, he returned to the cove and thereafter patrolled only in the cove. Apparently the cove was ultimately more attractive than the frond in open water.

The size of each territory varies according to the influence of several different factors which are not well understood. It is clear that larger males hold proportionally larger territories than the smaller ones. From general observations it is also apparent that territories are small when the population density is high, and large when the population density is low. On the other hand territories may be large in the midst of the breeding season when pupfish are numerous. This seems to result from a disinclination of most of the males to fight for territories during those periods. The few aggressive males dominate large areas with little need to defend them. For instance, on 4 June 1955, individual territories reached the relatively enormous sizes of 5 to 6 square meters as compared to the customary size of about 1

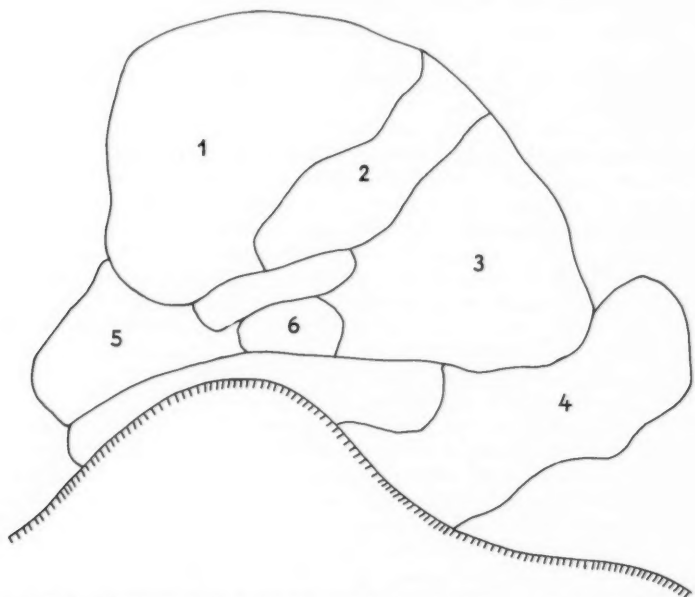


Fig. 2—Territories of six male pupfish. At the bottom of the sketch is the shore line. The enclosed area adjacent to the shore represents a patch of sand, approximately 1.4 m wide; the numbered subdivisions portray the territories, whereas the unnumbered subdivisions show the neutral areas.

to 2 square meters. The males were not particularly aggressive and chased intruders without the customary vigor. The intruders fled immediately. No spawning was seen, and one male forsook his territory during the hour of observation.

High temperatures also play a role in the regulation of territory size. On the afternoon of 5 August 1956, observations were made on a small (5 by 10 meters), densely populated pool (approximately 150 pupfish per square meter) with an almost uniform water temperature of 38.3°C. In larger pools pupfish can and do avoid temperatures over 36°C. to 37°C. (Barlow, 1958). It appeared that every member of the population of this pool was actively foraging. Most of the bottom was thickly carpeted with blue-green algae, but along the shore there was a patch of free sand about one and one-half square meters in area. The small sand patch contained territories of six different males (Fig. 2). Although the males did not actively patrol, their occasional forays indicated the boundaries of the territories and of the two neutral areas. Each male tended to stay in the center of his territory and plow and dig for food almost continuously. Three males with the smallest territories (number two, five, and six) tolerated females some of the time, and displayed by arching before attacking intruders. At different times the territory of male number six contained from 5 to 15 females. The males with small territories spent most of their time foraging, often responding to an intruding fish by merely raising the median fins without stopping foraging. The three males with the largest territories (one, three, and four) defended them vigorously; all intruders were driven out by a straight ahead charge. Once territory number four was overrun by about 40 females. The male holding this territory attacked them vigorously and it took him approximately 5 minutes to drive them out. Meanwhile yet another male next to the sandy region was defending an algal-coated area almost as large as the entire sand patch. He was constantly occupied with preventing the encroachment upon his territory by the many females and smaller males and thus was unable to search for food. At the high temperature of 38°C. it seems that pupfish are almost compelled by metabolic demands to seek food continuously. The time and effort expended by males in defending such large territories must handicap them in the competition for available energy. [*i.e.*, food.]

Apparently there was a constant threat of encroachment on the territories by the non-territorial pupfish. Yet male number one left his territory and stayed away for more than thirty minutes, during which time only one other fish entered this territory. Males number two and five observed the boundaries between their territories and that of male number one as though the latter were still present. Rarely male number two crossed the boundary, but quickly turned back. A new and smaller male entered the unoccupied territory after first foraging along its shoreward edge. After about 5 minutes the small male moved to the center of the territory and began returning

the displays of neighboring males. Then the small male deserted the territory, apparently without being driven off. The territory remained unoccupied.

The small sizes of the territories limited the activities of the males to such a degree that they tended to dig and plow in one spot only. Most of this excavating was done by plowing. The most interesting and rarely seen consequence was that small pits were built. Male number one made one pit and male number six excavated three adjacent depressions. Each pit had a raised lip and was about 2.5 cm deep and 6.5 cm in diameter. Nearby males whose territories were carpeted by blue-green algae were unable to dig pits. Since the bottoms of most of the shore pools of the Salton Sea are covered with algae it is not surprising that pupfish were never observed excavating pits at any other time.

Most male pupfish are the sole possessors of their territories. Not infrequently, however, constellations of smaller males are seen holding territories within that of a larger male. Observations made at 1700, 14 May 1955, are cited as one example. The territory of a large (45 mm long) male measured about 70 cm by 50 cm. The four smaller males which shared the territory ranged in length from about 20 mm to 25 mm. The boundaries of the subterritories were not distinct although the centers of activities of the small males were obviously within the territorial boundaries of the large pupfish. All five males drove off intruders, but not jointly. And the larger male drove off in turn each of the smaller males. The latter always fled after briefly circling with the larger pupfish. Then the dominant male resumed patrolling and within 2 to 3 runs across the main territory encountered and drove off another small male. By this time, however, the first small male had returned. The procedure repeated itself each time the dominant male encountered one of the smaller males. On most other occasions large males were seen to attack even smaller males (about 15 mm in length) that were already in nuptial coloration, although rarely they were tolerated. Juvenile pupfish often were tolerated within the territories.

AGGREGATING BEHAVIOR

Normal schooling behavior was never observed in the inadequate space of the aquaria. However, when the pupfish were first brought in from the field and placed in an aquarium they formed schools. The fish moved slowly over the bottom in troop-like columns, often near the wall of the aquarium. After the fish had acquainted themselves with the new surroundings this behavior disappeared.

Pupfish in shore pools and springs regularly move in schools and forage in groups. The schools are spread out in the horizontal plane, but not in the vertical; according to Keenleyside (1955) this is typical for fish schools. Females and juveniles school throughout the year, and the males school with them when not holding territories. During the breeding season males not infrequently are seen in the rear parts

of otherwise all female schools. Both sexes school together during the winter. However, during the coldest weather the fish sometimes spread out to such an extent that schools are barely recognizable as such.

Pupfish of different sizes usually do not school together. They segregate into groups in which the individuals are about equal in length. Observations of schools of mixed size groups revealed that sorting results from differences in swimming speed. The larger fish swim proportionately faster, and thus heterogeneous schools quickly fractionate because the smaller fish fall behind. Also, the smaller fish stay in shallower water, almost in proportion to their sizes.

Schooling plays a greater role in the social behavior of juvenile pupfish than it does in that of adult females. The females move about in smaller numbers and also separate from the school more readily. Juvenile pupfish have been observed in schools which were estimated to number upwards of 10,000 individuals. The cohesion of even small schools of juveniles can be appreciated from the behavior portrayed in Figure 3.

A remarkably different type of schooling behavior once was observed in a mixed school of about 300 female and juvenile pupfish. The school, traveling in a tight column close to the bottom, moved into a small channel (1 m wide and 5 cm deep) which connected two

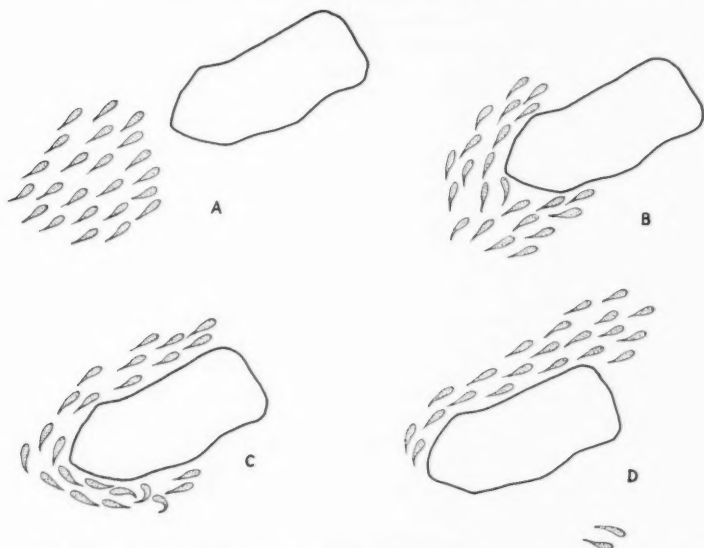


Fig. 3.—A school of juvenile pupfish in shallow water (about 2 cm deep) approach (A), and pass (B to D), a tiny island (about 10 cm long). The attraction the school holds for the individual is seen best in Panel C.

shore pools. A slight current was perceptible, but the water temperature was the same as that of each of the contiguous pools. Once in the channel the fish began to circle and formed a revolving disc-shaped school. They were uncommonly close to one another, often touching. Many different species of marine fishes which regularly school form similar compact whirling masses of fish when attacked by predators. Now and then the milling pupfish darted aside almost as one. This sudden darting, together with milling, was strikingly like the fright behavior of shoaling oceanic fishes. On the other hand the entire school of pupfish sometimes stopped suddenly and settled onto the bottom. Individuals nestled into the algal mat and lay almost motionless. They did not, however, burrow out of sight as pupfish sometimes do when escaping a net, but remained on top of the mat. Shortly thereafter they would jointly resume milling. This behavior, for which no explanation is forthcoming, lasted almost two hours.

While milling the pupfish showed marked avoidance of a shadowed area. A small pier cast a straight edged shadow which fell near the fish. If the school came up against the shadow, the near side formed a straight line along the shadow so that the fish remained in the sun-lit water. Breder and Rasquin (1950) concluded from their experiments that *Cyprinodon baconi* is, "practically light indifferent." It is not likely that two such closely related species would have such different responses to contrasting light intensities. Doubtless the environment and the emotional state of the fish can alter such responses. Breder (1959) has noted that young *Mugil trichodon* (Poey) are clearly wary of shadows in nature, but are photo-negative in the experimental choice box.

DISCUSSION

Many differences in behavior between pupfish in their natural habitat and those in aquaria could be pointed out. The obvious differences in territoriality and schooling behavior require no further comment. On the other hand, the prolonged pair bond seen between the fish in aquaria deserves further consideration. Without the benefit of field observations, one would conclude falsely that the male and female regularly form a pair which lasts for an hour or more. Further, one might think that nuzzling and meandering were important elements, not rare ones, of the reproductive behavior. Another difference is that the reaction of male and female to one another is immediate in the field. When the female is ready to spawn she seeks a fully receptive male. In the aquarium, however, the fish are suddenly together and then must become properly motivated. Thus the resident female at first attacks the introduced male. In other words, the spawning threshold is too high at first (or the fighting threshold is too low) and must be lowered before reproductive behavior can occur.

The female pupfish probably recognizes the male from his shape and color. In the shore pools females usually initiate the spawning at

the approach of a male. The ability of a female to discern, and respond to, a motionless male in a beaker of water also speaks for this argument. Nonetheless, movement by the male is doubtless also of importance.

The means by which a male pupfish recognizes a female are less clear. Breeding males attack other males, but not females, even though the female is not ready to spawn, but is only passing through his territory. Also, males do not usually attack juveniles. On the other hand, males in aquaria containing only other males occasionally spawn against their fellows. The male treated as a female is smaller, passive, and pale in color from being harassed. In the prolonged absence of a female the spawning threshold should be low. Consequently, otherwise inadequate stimuli could release this behavior. Koster (1948) observed in a free living toothcarp, *Plancterus kansae* (Garman), one male attempting to spawn against another male which was non-moving, though fully colored.

The brilliant nuptial dress of the patrolling male pupfish renders him conspicuous. And the coloration and behavior go hand in hand. As the male swims forward the movements of the orange caudal fin contrast sharply with the blue body. When the male stops, the orange pectoral fins are thrown forward and begin beating alternately. Thus the run-stop nature of patrolling shifts the flicker of orange back and forth between the pectoral and caudal fins. This type of display attracts the eye of the observer, and presumably also that of the female pupfish.

The black eyes of the male in breeding colors may be important clues in the orientation of the fighting behavior. Male pupfish start their fights facing one another, move into the eye to eye position, and then stand parallel, invariably head to tail. That they never stand parallel and head to head speaks strongly for the necessity of some structure which carries the information about the front and back ends of the opponent. Just moving ahead is not enough; one or the other male often starts circling at this time so that the other must continually orient itself to its opponent. The parallel and head to tail position can be observed in the fights of several other kinds of fishes. But many species go from the facing stance to a parallel position which is sometimes head to tail and other times head to head. This can be seen especially well in the common aquarium cyprinid *Brachydanio rerio* (Hamilton). The behavior of a reasonably close relative of the desert pupfish, *Fundulus notatus* (Rafinesque), however, suggests that the eye is not necessarily important in orienting rival males to one another. As described by Carranza and Winn (1954), *F. notatus* males orient head to tail even though the eye is obscured by a black horizontal line passing through it.

The color of the caudal fin also might play an important role in the fight between two male pupfish. Once they are head to tail they begin tail-beating and each sees only the orange caudal fin of the

opponent. The size and color of the tail could augment the effect of the tail-beats in intimidating the rival male.

The color pattern and behavior of the desert pupfish, *Cyprinodon macularius*, appear to be among the simplest kinds known within the toothcarps. As can be seen in any good aquarium book, male toothcarps can be arranged in a series according to the increasing ornamentation of the caudal fin and the borders especially of the median fins. One can proceed from the almost uniformly orange caudal fin found in the desert pupfish to the beautifully adorned species of *Aphyosemion*. In the closely related species, *Cyprinodon variegatus*, the caudal fin is orange, but is also bordered with black (Raney *et al.*, 1953). On the other hand, the color pattern of *Cyprinodon nevadensis* Eigenmann and Eigenmann, once considered conspecific with *macularius*, is of an even simpler type: the caudal fin is the same dark blue as the body (Miller, 1943). It would be of interest to know which selective pressures were more effective in producing these elaborate structures — intimidation of rival males, or selection by the females. The complexity of the body markings also proceeds well beyond the simple blue of the desert pupfish.

An overwhelming number of male toothcarps have brightly colored pectoral fins when reproductively motivated. It is extremely unusual for the pectoral fins of free-swimming fishes to be conspicuously colored. In most fishes, excluding the bottom living forms, the pectoral fins are hyaline. These fins are normally in constant motion to counteract the opercular jets. Moreover, they are frequently the fins most used in the normal activities of fishes. The bright markings are commonly carried on the median fins which are used less often in moving about. *Anabas testudineus* (Bloch), a labyrinth fish, and pomacentrid fishes of the genus *Amphiprion* constitute rare instances of fishes with colorful pectoral fins outside the Cyprinodontidae. Judging from its widespread occurrence, the flickering of conspicuous pectoral fins is a long established behavioral characteristic in the Cyprinodontidae.

The spawning posture of cyprinodontid fishes is a splendid pre-adaptation to viviparity. Rosen and Gordon (1953) have shown that the anatomy of the anal fin of the male adumbrates the evolution of the gonopodium. It is not surprising that viviparity has arisen independently within the Cyprinodontiformes at least five times, namely in the Adrianichthyidae, Anablepidae, Goodiidae, Jenynsiidae, and Poeciliidae. Many intermediate forms are known, such as *Cubanichthys*, *Horaichthys*, and *Oryzias*.

A comparison of the behavior of the desert pupfish with that of the viviparous fishes of the related family Poeciliidae will not be undertaken here. The behavior of the members of the other viviparous families is almost unknown. The reader may wish to compare the behavior of the desert pupfish with that which is known for the Poeciliidae. The article by Wickler (1957) should be useful in this respect since it treats several species of Poeciliidae.

Within the Cyprinodontidae the spawning behavior of the desert

pupfish appears to represent one of the simplest types. As with most of the toothcarps the spawning position is one in which the pair is upright, parallel, touching, S-shaped, and facing in the same direction. Unfortunately most of the information concerning the spawning behavior of cyprinodontid fishes is scattered in the literature of the aquarist, and often is in an unusable form. Nonetheless, certain types of variation are reliably evident. In some species the pair bores into the bottom (for instance, *Cynolebias*, *Pterolebias*), in others into plants (*Epiplatys*). Sometimes the spawning position includes laying over on the side, usually with the male on top (*Plancterus*, Koster, 1948). The coming together of males and females is also usually more circuitous than observed in the desert pupfish.

The complex mating ethogram of *Oryzias latipes* (Temminck and Schlegel) has been described by Ono and Uematsu (1957). Although *Oryzias* and *Cyprinodon* are not closely related, certain aspects of their behavior are remarkably similar. Ono and Uematsu have named the constituent motor patterns in *Oryzias* and listed them in their customary sequence of occurrence. The motor patterns, with their possible counterparts in the pupfish, are given in the intended sequence, but those movements peculiar to *Oryzias* are omitted: "pecking up" — nuzzling, "floating up" — sidling, "crossing" — wrapping, "copulation" — S-shaping, and "spawning" — jerking. Of the foregoing, the correspondence between "pecking up" and nuzzling seems the least certain.

The ethology of *Cyprinodon macularius* described in this article and that of *C. variegatus* as reported by Raney *et al.* (1953) appear to be essentially similar. Since these authors did not describe most of the motor patterns, little more can be said. In one respect, however, the two species doubtless differ. The males of *variegatus* make pits in their territories, most often near the territorial center. This "nest" is a roughly circular pit, 10 to 15 cm in diameter, and 2.5 to 4 cm deep. Spawning within the "nest," however, is unusual. The males of another American toothcarp, *Jordanella floridae* Goode and Bean, also make pits which are not used as incubation sites for the eggs (Peters, 1941). Males of *C. macularius* build pits only under certain conditions which have been described in the preceding. Even then the pits are appreciably smaller (about 6.5 by 2.5 cm) than those reported for *variegatus*. It might be pertinent to mention that *macularius* occurs in desert pools which seldom have a substrate suitable for pit building. Perhaps the environment has selected against this behavior in the desert pupfish.

Nipping the substrate by the female also calls for comment. This movement reveals the female pupfish definitely is ready to spawn. The motivation, therefore, is predominantly sexual. But in its form nipping clearly is eating behavior, or an only slightly modified version of it. The movement, or associated movements, differ enough from normal eating behavior to enable the male to distinguish a receptive

female within a group of foraging females. I suspect the clue lies in the way the female drops her abdomen to the bottom as she completes the nipping, as well as in the more emphatic expression of the nipping movement itself. Females usually are foraging when they encounter a male. It seems that the principle foraging movement has been slightly exaggerated and stereotyped to signal readiness to spawn.

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Eighteen New Species in the Genus *Calicurgus* Lepeletier (Hymenoptera: Psammocharidae) from Mexico, Central and South America with a Key to All the Species and Photomicrographs of the Male Genitalia and Subgenital Plates

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ABSTRACT: Eight new species are described from Mexico and Central America. The status of *Calicurgus hyalinatus* Fabricius is discussed. Nine new species are described from South America. Keys for all the known species for both sexes are given; a separate key is provided for each region. Photomicrographs of the genitalia and subgenital plates for the males of the new species and for three species previously described. A total of twelve species are treated for Mexico and Central America and twenty-three species from South America.

The genus *Calicurgus* is represented throughout most of world, but apparently the species are more numerous in the Neotropics. The species especially as represented by the genitalia and subgenital plate are a homogeneous group without too much variation in the structure. The keys are made up in two groups, one for Mexico and Central America and the Caribbean region and the other for South America. Key construction is simplified and they are easier to use when they are separate for each region. Dr. Henry K. Townes recently made a trip to the British Museum to study the type of Ichneumonidae and while there checked Cameron's types in the Cryptocheilinae. He found that *Salix teapensis* should be referred to the genus *Calicurgus* (private communication to the writer). The designations for places of deposit of the type specimens are listed below.¹

The Genus *Calicurgus* Lepeletier

This genus, one of the subfamily Cryptocheilinae, is diagnosed by the presence of straight sides of the basal abdominal segment and, in the female, teeth and spines on the outside of posterior tibiae. It is separated from the other genera by the following characters: (1) the front of the pronotum is perpendicular to the dorsal surface; (2) the anterior tibia in the female has a very noticeable spine on the dorsal apex (not so noticeable in the male); (3) the male has a

¹ Location of types: USNM = U.S. National Museum; MCZ = Museum of Comparative Zoology, Harvard University; MSU = Michigan State University, East Lansing, Michigan; RRD = R. R. Dreisbach, Midland, Michigan; Cal. Acad. = California Academy of Science, Golden Gate Park, San Francisco; Kan. = Entomology Museum, University of Kansas, Lawrence; Cal. = State Dept. of Agriculture, Sacramento 14, California.

characteristic genitalia and subgenital plate in that the volsellae have a double pair of basal hooklets on the inside edge near the base; (4) in both sexes the eyes converge strongly above; (5) the basal and transverse veins in the fore wings are either interstitial or only slightly disjointed; and (6) the subdiscoidal vein in rear wings is either interstitial with cubital vein or slightly basad of it (generally from one to two times the thickness of a vein).

In the descriptions, number in parenthesis after the lower or upper interocular distance is the comparative length on the same scale as the ratio of the lengths of the first antennal joints. This is measured by a scale in the eyepiece of the microscope and the scale is 100 divisions = 1.325 mm.

Mexican, Central American and Caribbean Species

Calicurgus flavidus n. sp.

Holotype female.—Body completely black, except apical half of mandibles are reddish; legs beyond tibiae are brownish; sides of face to base of antennae with beautiful yellowish pubescence; sides of pronotum and across the posterior border with similar pubescence but not quite so yellow; the ventral surface of fore coxae, and the outer posterior corners of propodeum with a narrow band across the extreme apex the same color as face; the rest of thorax and legs with pubescence silvery; clypeus with a broad ($0.3 \times$ length of clypeus) shiny, hairless apical edge, which does not quite reach the sides; the apex of this apical edge with a very narrow smooth apical margin, the surface back of margin like rest of clypeus, opaque, hairy and with coarse punctures; this punctured edge of front margin about $0.45 \times$ width of clypeus; clypeus $2.3 \times$ broad as long; eyes strongly converging above, the lower interocular distance (95) $1.45 \times$ that of upper (65); interocular distance at middle, $0.52 \times$ the transfacial; head $1.25 \times$ as broad as long; lateral ocelli slightly closer to eyes than to each other (ratio 12:15); ratio of length of first 4 antennal joints is 35:8:70:60; front mat punctures almost touching, those on mesonotum slightly farther apart, surface opaque; pronotum transverse behind; propodeum short in a smooth curve from base to apex, no dorsal hair, except at lower outside corners; wings strongly banded over basal veins and a broader band over cubital cells, covering the marginal, second and third cubital cells and extending to rear edge of wing but hardly noticeable behind discoidal cell; the first band about as wide as third cubital cell, starting at base of basal vein and at subcostal vein; second and third cubital cells of equal length on marginal vein but third the longest below; the second recurrent vein strongly bent outward in the middle; the basal vein in fore wing basad of the transverse by a little more than $0.4 \times$ the length of latter; the pulvillus of claws large, subparallel-sided to about middle and the apical half triangular with a broad apex; apical half of pulvillus black; the apical black-shining edge of clypeus has four rather strong

lengthwise wrinkles; length head and thorax 4.0 mm, abdomen 2.7 mm, fore wing 8.7 mm, rear wing 7.1 mm.

Type locality.—Cuernavaca, Morelia, Mexico, June, 1945, N. L. H. Kraus (USNM).

Paratypes.—One, 4 miles E. of Cuernavaca, Morelos, Mexico, 6000', June 20, 1959 (RRD); another, same data but date, June 25, 1959 (Evans).

***Calicurgus niger* n. sp.**

Holotype female.—Completely black, except a tinge of dark red on apical half of mandibles; only thin fine pubescence on body, no shiny pubescence spots; clypeus like that of *C. flavidus* but front edge not as wide nor as smooth, and with a few more not so coarse wrinkles, clypeus $1.3 \times$ as broad as long; eyes strongly convergent above, lower interocular distance (80) is $1.33 \times$ the upper (60); head slightly broader than long; middle interocular distance $0.57 \times$ the transfacial distance; ratio of length of the first 4 antennal joints is 35:15:60:55; lateral ocelli as far from eyes as from each other, front and mesonotum like *flavidus* but more shining; wings banded like *flavidus* but the bands not as dark and the one over the basal veins narrower; cubital cells like *flavidus*; the basal and transverse veins in fore wings are interstitial; antennae much more slender than that of *flavidus*; pulvillus of claws the same shape as *flavidus*, but apical half white; length of head and thorax 3.3 mm, abdomen 3.0 mm, fore wing 6.0 mm, rear wing 4.3 mm.

Type Locality.—S. Andres Tuxtla, Vera Cruz, Mexico, October 25, 1957, R. and K. Dreisbach (USNM).

***Calicurgus cruralis* n. sp.**

Holotype female.—Ground color of body black, but with a deep reddish cast to the thorax, basal two abdominal segments and the posterior edge of third segment; the clypeus and mandibles a little brighter reddish; all the legs including coxae, trochanters, and apical tarsal joints a light to dark reddish; antennae wholly yellowish; a broad shining apical rim of clypeus, a narrow smooth edge and the rest of hairless rim with coarse lengthwise wrinkles, clypeus almost $3.0 \times$ as broad as long, the hairless rim less than $0.3 \times$ length in middle and becoming obsolete at sides; a number of long hairs extend from center of clypeus beyond the hairless rim; clypeus, face and lower front silvery sericeous; the whole thorax and abdomen with a thin fine silvery pubescence, which in places appears more as a bloom than a pubescence; head $1.2 \times$ as broad as long; the middle interocular distance $0.56 \times$ the transfacial the upper interocular distance (60) is $0.6 \times$ the lower; ratio of length of first 4 antennal joints is 35:15:65:55; lateral ocelli as far from eyes as from each other; wings hyaline, veins yellow, a dim cloud over basal veins (from subcostal vein backward, which fades out before reaching the hind margin of wing) and over cubital cells; the subapical cloud covers the marginal, second and third cubital cells and about one half of the

discoidal cell back of them; these clouds are very faint; basal and transverse veins in fore wings interstitial and the subdiscoidal vein in rear wing basad of cubitus by about $2.0 \times$ the thickness of vein; a few long hairs on sternum of abdomen from about fourth sternite with an increase of long light hairs on last segment; length of head and thorax 4.0 mm, abdomen 3.3 mm, fore wing 7.2 mm, rear wing 5.3 mm.

Type Locality.—Balboa, Canal Zone, Panama, May 13, 1914, T. Hallinan (MCZ).

***Calicurgus argutus* n. sp.**

Holotype female.—Whole body black, with the legs having a slight brown color; face, clypeus, spots on sides of thorax, base of propodeum and lower sides of propodeum with a slight silvery pubescence; apical half of mandibles reddish; a broad hair-less apical rim on clypeus is $0.4 \times$ the length of clypeus in the middle and narrows toward the side, disappearing at outer 0.2 of clypeus; clypeus $2.4 \times$ as broad as wide; upper interocular distance $0.7 \times$ the lower; middle interocular distance $0.6 \times$ the transfacial; ratio of lengths of the first 4 antennal joints is 25:15:55:45; lateral ocelli slightly closer to eyes than to each other; wings hyaline except for the two clouds, apex of wing clear; cloud over basal veins small and faint, beginning behind the junction of cubital and basal vein and widening in the second discoidal cell; the cloud over the cells is much darker and larger, and covers the marginal, second, and third cubital and most of third discoidal cell; basal vein in fore wing is basad of transverse vein by about the thickness of a vein; the subdiscoidal vein in rear wings is basad of cubitus by about $2.0 \times$ the thickness of the vein; length of head and thorax 3.3 mm, abdomen 2.6 mm, fore wing 5.3 mm, rear wing 3.9 mm.

Type Locality.—Acayucan, Vera Cruz, Mexico, Oct. 23, 1957, R and K. Dreisbach (USNM).

Paratype.—Guadalajara, Mexico, July 12, 1959, 5000', H. E. Evans (Evans).

***Calicurgus major* n. sp.**

Holotype female.—Completely black except for some reddish color on middle of mandibles, and the reddish colored spines on all the tarsal joints; strongly silvery sericeous on clypeus and face, but not on front or vertex; strongly sericeous on under side of thorax and on ventral surface of coxae; sides of thorax, and across the basal and apical surface of propodeum are strongly sericeous; the surface across middle of propodeum lacks this pubescence; the dorsal surface of propodeum, and the subcostal cell and stigma has a dull greenish color; the apical third of clypeus hairless, deep black and shining, with about 5 very large shallow pits or punctures; the hairless apical margin narrows toward the sides and becomes obsolete before reaching sides; clypeus $2.6 \times$ as wide as long; head $1.25 \times$ as broad as long; middle interocular distance $0.56 \times$ as long as transfacial; lower

interocular distance (140) $2.0 \times$ the upper (70), thus the eyes very strongly converging above; ratio of length of first 4 antennal joints is 55:20:120:100, thus third antennal joint is $1.4 \times$ as long as upper interocular distance; lateral ocelli slightly farther from each other than from the eyes (17:13); wings bifasciate with dark color; the basal band starting at subcostal vein, narrow there and expanding to greatest width at the submedian vein where it is as wide as second and third cubital cells and irregular on both edges; the band over cells covers marginal, second and third cubital and most of apical half of third discoidal cells; second recurrent vein bowed outward in the middle; tip of wing beyond cells snow-white; the wing hyaline except for the bands and apical spot; pronotum transverse on posterior edge; slight silvery pubescent spots on sides of second, third and fourth tergites; the abdomen with a slight greenish tint; posterior tibiae with 10 teeth on basal 0.75, concave on front, located on center of dorsal surface at a slight angle and with a spine behind them; another row of spines occur close to them on inner side and a row of smaller reddish spines on the outside but not so close to teeth; length of head and thorax 6.6 mm, abdomen 5.6 mm, length fore wing 11.6 mm, rear wing 8.6 mm.

Type Locality.—Mexico, Vera Cruz, Vulcan, San Martin, SE. slope 4000', July 22, 1959, at light, B. T. B. Valentine (USNM).

***Calicurgus pruinus* n. sp.**

Holotype female.—Black; apex of mandibles reddish and apex of fore tibiae and the apices of fore tarsal joints yellowish; all tarsal joints with yellowish pubescence and reddish spines; clypeus and face strongly silvery pubescent, the front with pubescence not nearly so dense; posterior orbits and sides of thorax and propodeum (except central part) are silvery pubescent; abdomen pruinose; lower side of pronotum and just below the shoulders possess two spots of pubescence (in certain light) which have a yellowish tint; apical edge of clypeus bare and with about 10 rather broad smooth longitudinal ridges; clypeus $3.0 \times$ as wide as long; lower interocular distance (90) $1.8 \times$ the upper (50); middle interocular distance $0.58 \times$ the transfacial; head $1.2 \times$ as broad as long; lateral ocelli as far from eyes as from each other; ratio of length of first four antennal joints is 40:15:70:60; pronotum transverse behind (very slightly concave); propodeum very short in a steep curve; wings bifasciate, with two dark prominent bands; the basal band, irregular on front and rear, starts just basad of basal vein and is about $0.67 \times$ as wide as the length of the second and third cubital cells on the marginal vein; the second band covers the marginal and extends to rear of wing about width of the marginal cell; the rest of wing slightly yellowish with a snow-white tip just beyond third cubital cell; quite a few long light hairs are present on the last abdominal segment, a few on the rest of the ventral segments; length of head and thorax 3.6 mm, abdomen 3.3 mm, length of fore wing 6.9 mm, rear wing 5.6 mm.

Type Locality.—Acayucan, Vera Cruz, Mexico, Oct. 23, 1957, R. R. and K. N. Dreisbach (USNM).

Paratype females: Three, same data as holotype (R.R.D.); One, Yucatan, G. F. Gaumer (Kan.).

***Calicurgus albosignus* n. sp.**

Fig. 1

Holotype male.—Mostly black with the exceptions as noted below; clypeus, mandibles (except light reddish apex), mouth parts, apical 0.75 of ventral surface of fore coxae, posterior edge of pronotum, the lower front corners of pronotum, last tergite, all tibial spurs, and a ring around base of posterior tibiae, white; all femora (except extreme base of fore pair), first 2 pair tibiae (second pair slightly dark), and under side of antennae, rufous; fore tibiae blackish on last 3 joints and all of the last 2 pair black, as well as the last pair of tibiae (except basal ring); face and clypeus slightly silvery sericeous, little pubescence or hair elsewhere on body; head $1.3 \times$ as broad as long; upper and lower interocular distance equal (48); the interocular distance in middle of front greater (55); wings hyaline, no trace of a cloud; basal and transverse vein in fore wings almost interstitial, first recurrent meets second cubital cell at center, the second meets third cubital cell beyond middle; subgenital plate of the usual rectangular shape but genitalia is much different; parameres not scalloped and with a concavity outside but straight sided with a row of thick hairs on inside apical half; volsellae short, with a broad blunt apex and no sharp tooth on inside near middle; length head and thorax 3.0 mm, abdomen 2.6 mm, fore wing 4.3 mm, rear wing 3.3 mm; genitalia 0.66 mm, width 0.53 mm, length subgenital plate 0.78 mm (including stem), width 0.26 mm.

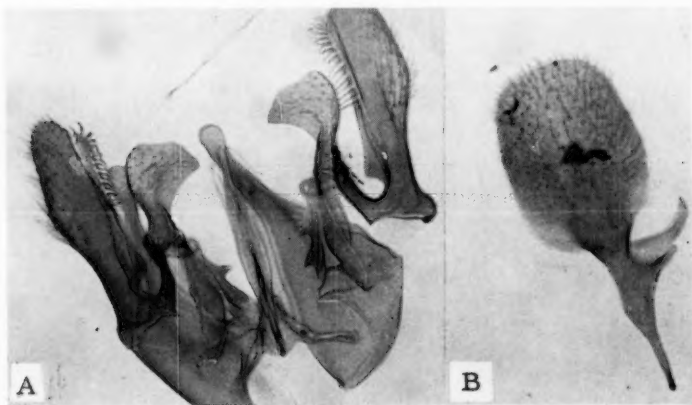


Fig. 1.—*Calicurgus albosignus*, n. sp. A. Genitalia ($\times 80$).
B. Subgenital plate ($\times 60$).

Type Locality.—Summit, Panama Canal Zone, October, 1946, N. L. H. Kraus (USNM).

Calicurgus aberrans n. sp.

Holotype male.—Body black except as noted; apex of mandibles reddish; a spot on ventral apex of fore tibiae, last tergite and tibial spurs white; apex of fore femora in front rufous; fore tibiae yellowish underneath, black above; first 3 joints of fore tarsi slightly yellowish, the last 2 pair tarsi slightly brownish; antennae wholly black; face and clypeus silvery pubescent and some silvery pubescence on mesopleura; clypeus with a narrow hairless rim and truncate across apex; clypeus a little more than $2.0 \times$ as broad as long; head as broad as long; middle interocular distance $0.61 \times$ the transfacial distance; the lower interocular distance (65) slightly greater than the upper; lateral ocelli about as far from eyes as from each other; a weak narrow infuscation over basal and transverse veins in fore wing, very short; a strong band over marginal, second and third cubital and apical third of third discoidal cells; rest of wing hyaline with the apex beyond cells hyaline but not snow-white; first and second recurrent veins meeting second and third cubital cells, respectively, beyond middle and at middle; subgenital plate differs from those of other species in genus, in being broader at apex than base; genitalia also much different; the parameres have a broad flange outside at base; volsellae end in a plate (not in a point as other species) with long hairs, and no spine on their inside near middle; the basal booklets at base of volsellae are very small, almost obsolete; the parapenial lobes are expanded at apex.

Type Locality.—San Cristobal, Casas, Chiapas, Mexico, April 30, 1959, 7500', H. E. Evans (USNM).

Paratype Males.—Three, same date as type (H. E. Evans); One, Rosario, San Juancito Mts, Honduras, 4800-5150', July 29, 1930, Hond. Exp. (ANSP); One, 4 miles E. Cuernavaca, Morelos, Mexico, June 7, 1959, 7500', (H.E.E.),

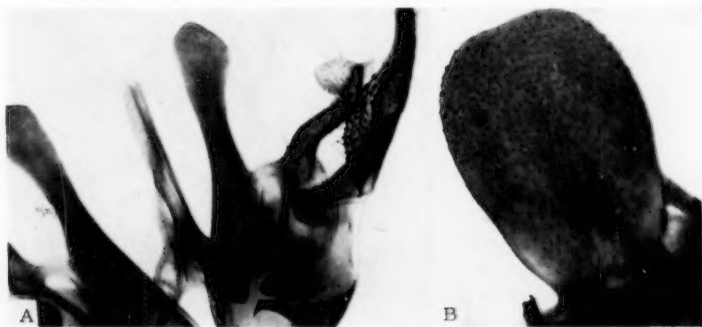


Fig. 2.—*Calicurgus aberrans*, n. sp. A. Genitalia ($\times 58$).
B. Subgenital plate ($\times 58$).

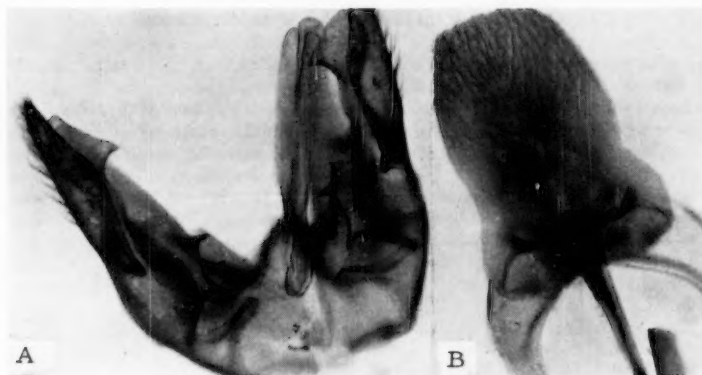


Fig. 3.—*Calicurgus hyalinatus* (Fabricius). A. Genitalia ($\times 62$).
B. Subgenital plate ($\times 62$).

June 2, 1959, 6000'; H. E. Evans (R.R.D.) ; One, Cuernavaca, Morelos, Mexico,
June 7, 1959, 5500' (Evans) ; One, San Cristobal 1), Casas, Chiapas, Mexico,
April 25, 1959, 7500', H. E. Evans (Evans).

Calicurgus hyalinatus (Fabricius)

Fig. 3

Townes (1957) considered the European *Calicurgus hyalinatus* (Fabricius) as conspecific with the polytypic Nearctic species *C. alienatus* Smith. If only the external anatomy is examined there is no reason to consider them as distinct species. However, when the genitalia is examined there is a major difference between these two entities. The volsella of the Nearctic species and the three subspecies has a strong sharp tooth about the middle of the concavity on the inside edge. This tooth is sharp and strong (Fig. 4). On the other hand the Palearctic *C. hyalinatus* has not even the trace of a tooth (Fig. 3). For this reason, I consider these entities as distinct species.

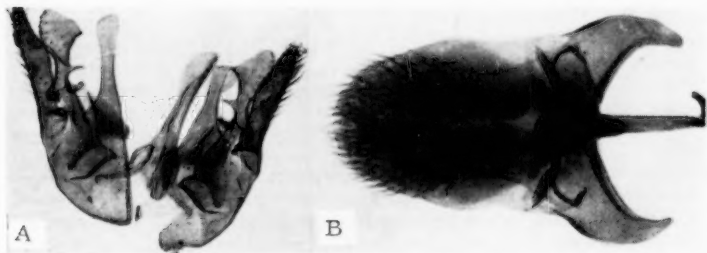


Fig. 4.—*Calicurgus alienatus alienatus* (Smith). A. Genitalia ($\times 60$). B. Subgenital plate ($\times 60$).

Key to Mexican and Central American
Females

1. Abdomen entirely black 2
1. Abdomen with at least the basal two segments ferruginous 9
2. Legs completely rufous, including coxae, trochanters and tarsi (completely); fore wings with a very faint cloud over the basal veins (beginning just basad of basal vein) its length equal to length of second cubital cell on marginal vein; a similar faint cloud over all the marginal cell the second and third cubital cells and the discoidal cell just behind them; otherwise wings hyaline; basal and transverse veins in fore wings interstitial; antennae wholly yellow. Panama. *cruralis* n. sp.
2. Legs black or fore tibiae and tarsal joints very slightly brownish; at least the cloud over the cubital cells is very strong and dark; or whole wing dark 3
3. Fore wings practically wholly dark from base or close to base, an apical dark cloud and a preapical whitish band; a light streak part way across wing just back of base of stigma; rear wings fuscous. *alienatus excoctus* Townes
3. Fore wings with a cloud over basal veins and another over marginal and cubital cells or the basal cloud absent or almost so 4
4. Cloud over basal veins very faint and starts back of junction of basal and cubital veins, becoming wider as it extends backward; basal vein basad of transverse by less than the thickness of a vein; the subdiscoidal vein in rear wings basad of the cubitus by about twice the thickness of a vein; only strongly sericeous on the anterior orbits on the face (from antennae to eyes). Mexico. *argutus* n. sp.
4. Cloud over basal veins strong and dark, the cloud extending over the junction of the basal and cubital cells to the subcostal vein; the cloud over the cubital cells stronger 5
5. The dense glistening pubescence on sides of face and across posterior edge of propodeum (especially) with light golden color; apical 0.25 of clypeus hairless, shining and with lengthwise wrinkles (about 5 large ones); apex of wings beyond cells snow white in reflected light; the basal vein basad of transverse in fore wings by width of vein, in rear wings subdiscoidal basad of cubitus by width of vein; basal cloud only as wide as length of second cubital cell on marginal vein. Mexico. *flavidus* n. sp.
5. The pubescence silvery with no trace of golden color; clypeus with or without the wrinkles 6
6. Basal cloud as broad as the combined lengths of second and third cubital veins on marginal cells, and full width straight across wing; front with a silvery pile, thorax white with silvery pile; legs densely silvery-pruinose; first transverse cubital vein slightly elbowed at base; almost 11.0 mm long. Mexico. *teapensis* Cameron
6. Basal cloud not much broader than length of second cubital cell on marginal vein; legs not densely silvery-pruinose; front and sides of thorax not as strongly silvery as in preceding; much smaller size, less than 10.0 mm long 7
7. Rather strongly silvery, the abdomen pruinose; lower interocular distance 1.5× the upper; in reflected light wing shows up strongly dark in banded area; intermediate in size between the next 2; lateral ocelli slightly nearer each other than to the eyes; size 7.0 to 10 mm. Mexico. *pruinosis* n. sp.
7. Not silvery pubescent, (1) upper and lower interocular distance same as above and lateral ocelli same as above; size smaller, or (2) if size larger then lower interocular distance is 2.0× the lower 8

8. As in (1) above, size less than 7.0 mm; black area over cubital cells covering a greater part of wing. Mexico. *niger* n. sp.
 8. As in (2) above, size 12.2 mm. Mexico. *major* n. sp.
 9. Abdomen black apically; posterior tibiae with some infuscation at its apical one-quarter. U.S. and Mexico. *alienatus alienatus* Smith
 9. Abdomen entirely rufous; posterior tibiae entirely rufous except for a little darkening on its apical one-tenth. U.S. and Mexico. *alienatus rupex* Cresson

Males

1. Femora and tibiae of middle and hind legs black 2
 1. Femora and tibiae of middle and hind legs more or less ferruginous 3
 2. Posterior margin of pronotum with a white band; wings *not* bifasciate, with a narrow dark band over basal veins and a very prominent one over marginal and second and third cubital cells; front tarsi and front of fore tibiae tan, tibial spurs and a spot on rear apex of front tibiae white; parameres with a sharp point on inside of apex and one about middle on inside; subgenital plate almost rectangular. U.S. and Mexico. *alienatus excoctus* Townes
 2. Posterior margin of pronotum black; wings bifasciate, with a narrow rather faint band over basal veins and a strong one over the cubital cells; fore tarsi and *hind* part of fore tibiae tan, with fore part of front tibiae darker; parameres very blunt and broad at apex on inside and no trace of tooth on inside near middle; the 2 basal hooklets near base on inside of volsellae hardly more than indicated almost obsolete; subgenital plate wider at apex than base; spurs white. (Fig. 2.) *aberrans* n. sp.
 3. Clypeus entirely white; the fore coxae white on apical 0.75 underneath and a white spot on lower front corners of pronotum; all femora ferruginous except extreme base of first pair are fuscous; genitalia with parameres straight sided and with a row of short thick hairs on inside on apical half; apex of volsellae blunt without a tooth and no sharp tooth about middle on inside; basal hooklets on base of volsellae very small. (Fig. 1.) *albosignus* n. sp.
 3. Clypeus with some black; fore coxae without white; no white spot on lower front corners of pronotum; femora generally with more infuscation; parameres with a deep concavity on outside; volsellae with an acute tooth at apex and also one on inside near middle; the 2 pair of basal hooklets strong 4
 4. Femora, tibiae, fore and middle tarsi fulvous to light brown; the femora basally infuscate; the middle and especially the hind tibiae, more or less infuscate apically and basally; the extent of basal infuscation on femora varies from a narrow basal ring to more than 0.6 the length; the infuscation is usually most extensive on front femora. U.S. *alienatus borealis* Banks
 4. Colored as in *borealis* except for an average smaller extent of infuscation on femora and tibiae. (Fig. 4.) *alienatus alienatus* Smith and *alienatus rupex* Cresson

The South American Species
Calicurgus ruficrus n. sp.

Fig. 5.

Holotype male.—Head, thorax and last four abdominal segments black; clypeus except central 0.25 white; a yellowish posterior border

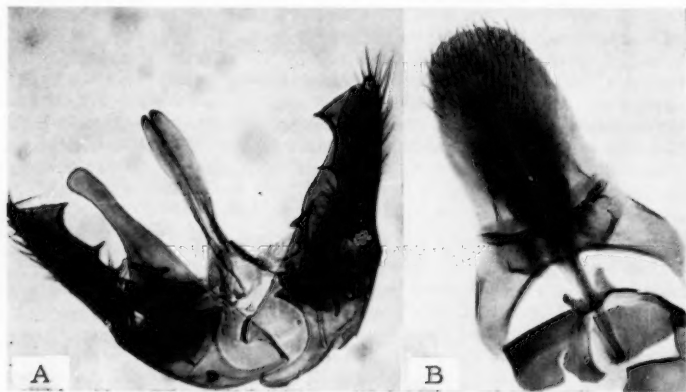


Fig. 5.—*Calicurgus ruficrus*, n. sp. A. Genitalia ($\times 80$).
B. Subgenital plate ($\times 80$).

on pronotum; ventral surface of first abdominal segment rufous as well as all the second and third (posterior border of second and third segment and dorsal surface of first blackish); last tergite with a dorsal white spot; mouth parts yellowish; all trochanters, femora and tibiae rufous; fore coxae mostly blackish, the last 2 pair rufous; last joint of first 2 pair tarsi brownish; last pair completely brown, as well as apex of last pair tibiae; first pair spurs whitish, the last 2 pair almost pure white; upper and lower interocular distance equal (55); wings hyaline, the third intercubital vein rather suddenly bent forward thus making third cubital cell shorter on marginal vein than the second, about $0.6 \times$ as long; basal and transverse veins in fore wings slightly disjointed; thorax very finely, silvery pubescent; antennae black above, brown beneath; lateral ocelli as far from eyes as from each other; head, front, and mesonotum finely punctured; genitalia and subgenital plate similar to *C. hyalinatus alienatus*; length head and thorax 3.0 mm, abdomen 3.0 mm, fore wings 5.3 mm, rear wings 4.0 mm, length genitalia 0.53 mm, width 0.26 mm, length subgenital plate 0.33 mm, width 0.26.

Type Locality.—Nova Teutonia, Santa Catarina, Brazil, November 29, 1955, Fritz Plaumann (Townes).

Paratypes.—Fifteen from Nova Teutonia, Santa Catarina, Brazil, Fritz Plaumann, with dates as follows: one, Nov. 27, 1956 (Townes); two, Nov. 29, 1955 and two, Nov. 26, 1953 (RRD) (Townes); one, Nov. 18, 1956 and four, Dec. 25, 1953 (Townes); one, Dec. 2, 1953 (Townes); one, Jan. 6, 1957 (MCZ); one, Dec. 3, 1955 (Townes); one, Dec. 25, 1952 (Townes); one, Dec. 4, 1955 (USNM); one, Nova Teutonia, Brazil, March 24, 1951 (Cal.).

Calicurgus unifascias n. sp.

Fig. 6

Holotype male.—Head, thorax, abdomen and legs black except

as noted below; mentum, white on sides of clypeus for about 0.6 of width, lower edges of pronotum, the outer posterior dorsal corners of pronotum, the last tergite of abdomen, the ventral apical half of fore coxae, the apical edge of basal spot on outside of posterior tibiae and the basal half of mandible (apical half reddish); last 3 joints of maxillary palpi and last 2 joints of labial palpi, white; basal 2 joints of maxillary palpi and basal one of labial palpi, brown; the first 2 segments of abdomen slightly reddish on sides; abdomen flattened; antennae black on dorsal surface and on first 2 joints beneath, rest brown beneath; front and vertex of head and thorax with a dull bluish color, shining; head and mesonotum very finely punctured; face, clypeus, and lower anterior orbits finely, silvery, pubescent; thorax and abdomen also finely pubescent; wings hyaline, with a faint, narrow darkening of the basal veins, and a fairly strong cloud covering the marginal cell, most of second and third cubital cells and extending into discoidal cell slightly; third cubital cell not quite as long as the second on the marginal vein but slightly longer than second below; basal and transverse veins in fore wings interstitial as are the cubitus and subdiscoidal in rear wings; upper and lower interocular distances equal (60) lateral ocelli as far from eyes as each other; genitalia distinctive, the parameres with three scalloped cross ridges on outside, and broader than usual; the volsellae without a sharp tooth about middle on inside; subgenital plate broader than usual; length of head and thorax 3.0 mm, abdomen 2.6 mm, fore wing 6.8 mm, rear wing 5.3 mm, length genitalia 0.79 mm, width 0.66, length subgenital 0.86 mm, width 0.40 mm.

Type Locality.—Nova Teutonia, Santa Catarina, Brazil, December 8, 1953, Fritz Plaumann (Townes).

Paratypes.—One, same locality, Dec. 26, 1952 (RRD); another, same locality, December 8, 1953 (USNM); two, V. Padro Monti (R. A. Tucuman-Burruyacu), 17.1, July 11, 1946, R. Golbach (MCZ) (RRD).

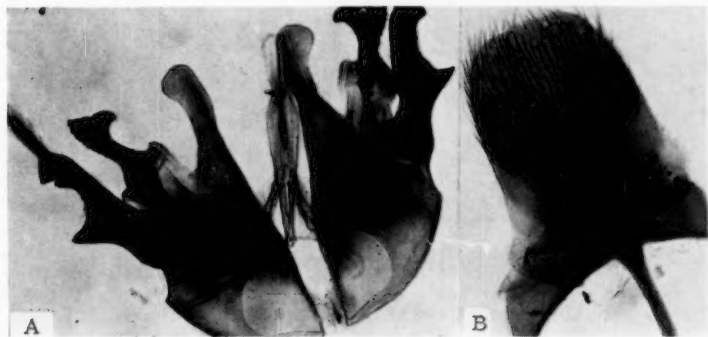


Fig. 6.—*Calicurgus unifascias*, n. sp. A. Genitalia ($\times 48$).
B. Subgenital plate ($\times 48$).



Fig. 7.—*Calicurgus anomalus*, n. sp. A. Genitalia ($\times 60$).
B. Subgenital plate ($\times 60$).

Calicurgus anomalus n. sp.

Fig. 7.

Holotype male.—Head black, thorax a dark brown, abdomen about same color as thorax but the sides and ventral surface of first 2 segments are yellowish; coxae, trochanters, and femora same color as thorax; outside of fore tibiae and last two pair of tibiae same color, except the last 2 pair tibiae have the dorsal base white; tarsal joints about same color, except first pair have their apex yellowish; a white stripe across posterior border of pronotum; sides of clypeus with white spots which do not quite reach base of clypeus, the color covering about 0.25 of width of clypeus; apex of fore coxae white; clypeus $2.5 \times$ as broad as long; middle interocular distance). $60 \times$ the transfacial; head $1.1 \times$ as broad as long; lower interocular distance (50) about equal to the upper; ratio of length of first 4 antennal joints is 25:12:22:22; lateral ocelli slightly nearer the eyes than each other; a stripe of silvery pubescence on anterior orbits above the white spots on side of clypeus which extends above base of antennae; very little pubescence on rest of body; pronotum transverse behind; wings hyaline slightly brownish; transverse and basal veins in fore wings interstitial, subdiscoidal in rear wings basad of cubitus; subgenital plate broad for its length; genitalia much more hairy than that of any other species I have seen from the western hemisphere; parameres very broad and flat, with long hairs on inside and around apex; these are visible and diagnostic without dissection; volsellae with the apex heavier and longer than usual and the spine on the inside about the middle hardly more than indicated where usually it is large and sharp; length head and thorax 3.6 mm, abdomen 3.0 mm, fore wing 5.3 mm, rear wing 3.4 mm, length genitalia 0.73 mm, width 0.50 mm, length subgenital plate 0.60 mm, width 0.33 mm.

Type Locality.—Nova Teutonia, Santa Catarina, Brazil, November 2, 1955, Fritz Plaumann (Townes).

Paratypes.—One, same locality, November 19, 1955 (RRD); two, same locality, January 10, 1956 and December 15, 1953 (Townes).

***Calicurgus ornatus* n. sp.**

Holotype female.—Whole body and legs black (exceptions noted below) with the patches of silvery pubescence making a beautiful appearance; apical half of mandibles a deep red; the patch of pubescence at apex of posterior tibiae, on the inside, reddish and tarsal joints are all slightly reddish with the apex of the joints slightly more colored than the other parts; the apical tergite also reddish; face, clypeus (except apical margin), and inner orbits to just above antennae with prostrate dense silvery pubescence in reflected light; the coxae, above and below, more or less, the mesopleura, and a band across apical half of propodeum (also a slight longitudinal band on dorsum) with strong glistening pubescence on sides and as streaks on dorsal surface; the clypeus with a black shining rim 0.4 of its length in middle which narrows and almost disappears at sides; clypeus $2.3 \times$ as broad as long; head not quite $1.2 \times$ as broad as long; lower interocular distance (115) almost $2.0 \times$ the upper (60), thus the eyes strongly converging above; interocular distance at middle $0.58 \times$ the transfacial distance; ratio of length of first 4 antennal joints is 60:20:95:75; lateral ocelli as far from eyes as from each other; pronotum almost transverse on posterior border but a slight indentation in center and a faint groove longitudinally on dorsum in center; wings hyaline but with two dark bands; the first band from subcosta backward over basal veins to rear of wing about $0.6 \times$ as wide as the one over cells; the apical band covers marginal cell, the second and third cubital cells and extends through the discoidal cell; basal vein slightly basad of transverse vein in fore wings by about the thickness of the vein; second and third cubital cells of equal length on marginal vein, but the third longer on base than the second; the second recurrent vein strongly bowed outward in the middle; the subdiscoidal vein in rear wing basad of cubitus by the width of vein; a few long hairs on propodeum, on apical margins of last three sternites, and on the last 2 tergites; posterior tibiae with 10 large concave teeth on dorsal surface, with a few fine hairs, shining and with a large spine behind each one, which is about $3.0 \times$ as long as the height of apex of tooth; a row of spines on outer edge of tibia as long as the spines behind teeth; the large spine on apical dorsal tip of fore tibiae is red on basal third, the rest deep black; the apex of tibiae is reddish; length head and thorax 5.0 mm, abdomen 6.3 mm, fore wing 8.8 mm, rear wing 6.9 mm.

Type Locality.—Monson Valley, Tingo Maria, Peru, October 26, 1954, E. L. Schlinger and E. G. Ross (Cal. Acad.).

Calicurgus anthracinus n. sp.

Holotype female.—A deep shining black, over the whole body including the coxae; trochanters slightly rufous especially below and on apex; all femora, tibiae and first 2 pair metatarsal joints rufous; last 4 joints of the first 2 pair legs and all the joints of last pair a reddish black; mouth parts, the fore coxae, and the apex of abdomen with considerable long hairs; a few long hairs on the posterior edges of all abdominal ventral segments; apical margin of clypeus hairless, shining and with a few longitudinal coarse wrinkles, for about 0.3 of length in center; the hairless rim becoming shorter at the sides; clypeus $2.5 \times$ as broad as long; head $1.1 \times$ as broad as long; middle interocular distance $0.66 \times$ the transfacial; lower interocular distance $1.33 \times$ the upper (90); lateral ocelli not quite $2.0 \times$ as far from eyes as each other; ratio of lengths of first 4 joints of antennae is 40:15:100:80; antennae entirely black; pronotum transverse behind; fore wings deep black with a brilliant violaceous reflection; rear wings deep brown without so much reflection; in fore wings basal vein basad of transverse vein by about $0.5 \times$ length of the latter; in rear wings the subdiscoidal vein is very slightly basad of cubitus; in fore wing third cubital cell is longer than second, the latter rectangular and longer than broad (55:80); the second recurrent vein strongly bent outward (angled) in the middle; length head and thorax 5.6 mm, abdomen 5.9 mm, fore wing 9.6 mm, rear wing 6.9 mm.

Type Locality.—Argentina, B. Aires City, March, 1950, M. A. Fritz (USNM).

Calicurgus semirufus n. sp.

Holotype female.—Head, thorax and last three abdominal segments black, the head and thorax dull, the last three abdominal segments shining with a bluish tint; the thorax also has a dull bluish luster in certain light; the first 2 abdominal segments rufous both above and below, except the extreme base of the first one is black; the first 2 segments are also shining; coxae black with bluish luster, the trochanters blackish with the tips rufous; all femora, tibiae and all tarsi (except last joint) same rufous color as base of abdomen; the apical 0.4 of clypeus with very large coarse punctures except the very narrow apical rim; clypeus $2.4 \times$ as broad as long; head $1.1 \times$ as broad as long; middle interocular distance $0.50 \times$ the transfacial; lower interocular distance $1.3 \times$ the upper (95); lateral ocelli slightly farther from eyes than from each other; ratio of length of first 4 antennal joints is 40:15:75:70; pronotum transverse behind, dorsal part very short; propodeum very short in a smooth steep curve, the dorsal part about $0.5 \times$ the posterior slope; fore wings very deep brown, rear wings brown but lighter; basal vein basad of transverse by less than width of vein, the subdiscoidal vein in rear wings basad of cubitus by the width of vein; second cubital cell almost square longer than wide by ratio of 10:9; third cubital cell almost $2.0 \times$ as

long as second; second recurrent vein in fore wings bent outward in a smooth curve; length of head and thorax 5.0 mm, abdomen 4.0 mm, fore wing 8.2 mm, rear wing 7.0 mm.

Type Locality.—Concepcion, Chile, 1904, P. Herbst (MCZ).

Paratype.—Chile, Varos (RRD); another, Angol, Chile, Dec. 22, 1956, Shoz (MSU).

***Calicurgus chilensis* n. sp.**

Fig. 8.

Holotype male.—Completely dull black, except for two white bands across the front of clypeus, just back of the narrow black hairless rim, which do not quite touch in middle; clypeus $2.0 \times$ as broad as wide; the white stripe covers about 0.25 of length of clypeus; the clypeus has a comparative width of 85, but the front quarter is suddenly narrowed at the posterior edge of the white band so that the part covered by the white band is only $0.7 \times$ as wide as the part between the eyes; the whole head densely covered with long black hair; the first antennal joint below and the upper side of all the coxae covered with some long hair; the pronotum and propodeum with shorter hair; face and clypeus with silvery pubescence; wings blackish; basal vein in fore wings basad of the transverse by the thickness of a vein, and in rear wings the subdiscoidal and cubital veins are interstitial; second cubital cell rectangular only slightly longer than broad, shorter than the third; third intercubital suddenly slightly bent inward at apex marking the length of third cubital cell on marginal vein only about 0.5 that on cubital vein; interocular distance in the middle $0.63 \times$ the transfacial; lower interocular distance (85) slightly greater than the upper (80); head $1.2 \times$ as broad as long, lateral ocelli $1.2 \times$ as far from each other as from the eyes; head and thorax length 4.6 mm, abdomen 5.0 mm, length fore wings 7.2 mm, rear

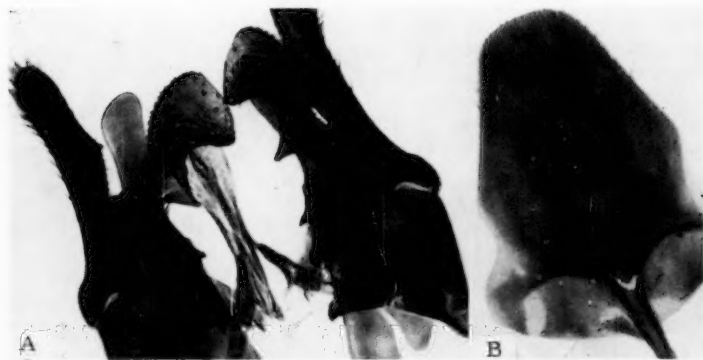


Fig. 8.—*Calicurgus chilensis*, n. sp. A. Genitalia ($\times 48$).
B. Subgenital plate ($\times 48$).

wings 6.0 mm, length genitalia 1.0 mm, width 0.66 mm, length subgenital plate 0.93 mm, width 0.46 mm.

Type Locality.—Angol, Chile, November 16, 1933 (MCZ).

Calicurgus fuscus n. sp.

Holotype female.—Body black, the thorax with a bluish tint or reflection especially on the front slope of pronotum and the sides of propodeum; the middle of mandibles reddish and a slight reddish tint on the fore part of clypeus; the posterior border of tergites 1-5, as well as posterior edge of the side pieces and a lengthwise streak on side of first tergite, rufous; the visible part of last tergite rufous; all coxae, trochanters (except yellowish apex), fore femora (except knees), about basal third of mid-femora and base of posterior femora black; all of rest of legs reddish; antennae yellowish brown; clypeus, face, fore coxae in front, mesopleura, sides of pronotum and most of propodeum (in certain light) finely densely silvery serviceous; the dorsal surface of pronotum only slightly silvery, and the vertical slope in front, hairless and shining; clypeus concave in front in middle, a rather broad, smooth, hairless semi-opaque apical margin back of which is an opaque rougher hairless shining surface which makes up one half the length of clypeus; just at base of this shining apical surface is a row of long thin hairs (about 20) which extend forward beyond the margin; clypeus $2.5 \times$ as broad as long and does not quite reach the eyes; head $1.15 \times$ as broad as long; middle interocular distance $0.6 \times$ the transfacial; lower interocular distance $2.0 \times$ the upper (60) thus the eyes strongly converging above; ratio of lengths of first 4 antennal joints is 50:15:90:70; lateral ocelli slightly farther from each other than from the eyes (15:13); dorsal surface of pronotum very short, posterior border transverse; very short dorsal surface on propodeum, slope steep, no upright hairs on surface; wings hyaline with a brown tinge; basal vein basad of transverse vein in

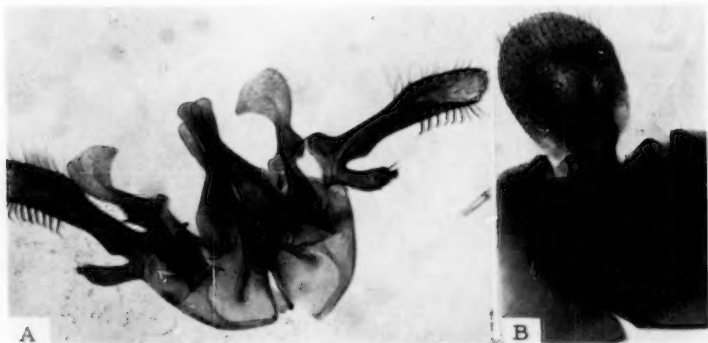


Fig. 9.—*Calicurgus modestus* (Smith). A. Genitalia ($\times 48$).
B. Subgenital plate ($\times 48$).

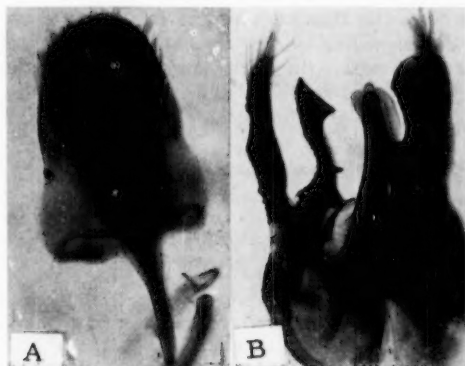


Fig. 10.—*Calicurgus rufigaster* Banks. A. Subgenital plate ($\times 50$).
B. Genitalia ($\times 50$).

fore wing by the width of a vein in rear wing subdiscoidal vein is basad of cubitus by about $2.0 \times$ the thickness of a vein; first intercubital vein is straight and slopes very strongly toward apex of wing, the recurrent veins meet their respective cubital cells at the apical and basal thirds respectively; nine very strong, concave, hairless teeth on middle of dorsal surface of posterior tibiae (on basal 0.6) behind the teeth is a strong sharp spine, $3-4 \times$ the length of teeth; a row of smaller spines on outer edge and a row of still smaller spines on inner edge; length head and thorax 4.6 mm, abdomen 3.5 mm, length fore wing 8.8 mm, rear wing 6.6 mm.

Type Locality.—Petropolis Rio, Brazil, March, 1938, Yellow Fever Service, MES Brazil, R. C. Shannon (USNM).

***Calicurgus braziliensis* n. sp.**

Holotype female.—Antennae, thorax, and head black except mouth parts are brown and the apical three quarters of the mandibles are reddish; abdomen black except basal two and one-half tergites are rufous on dorsum and sides, the first 2 ventrite mostly black, the third rufous; the last pair femora rufous, the first 2 pair slightly so at apex; all the tibiae rufous beneath, the first 2 pair black above, the last pair rufous on basal half above; tarsi blackish; a few long hairs on clypeus, under head, on ventral surface of abdomen and on last tergite; clypeus short, truncate in front, with a slightly turned up rim in front, almost $3.0 \times$ as broad as long; middle interocular distance $0.60 \times$ as long as the transfacial; head as long as broad; lower interocular distance (100) a little more than $1.2 \times$ the upper (65); lateral ocelli about as far from eyes as each other; ratio of length of first 4 joints of antennae is 35:15:60:45; pronotum with the dorsal surface a flat rectangle the posterior edge transverse; fore wing with section basad of basal veins and the apex beyond cells hyaline the space be-

tween dark brown, the rear edge of the fore wing is brown to base; rear wings with apical half darker than the hyaline basal half; dorsal surface of posterior tarsi with fairly large transverse plates (concave on front) as teeth on about basal 0.7, each tooth with a spine just behind it; length head and thorax 4.0 mm, abdomen 3.6 mm, fore wing 6.5 mm, rear wing 5.5 mm.

Type Locality.—Nova Teutonia, Brazil, April 23, 1951, Fritz Plaumann (Cal.).

Key to South American Species

Females

1. Abdomen with 2 basal segments rufous; wings black, or hyaline at base and apex with space between basal veins and apex of third cubital cell darker 2
1. Abdomen wholly rufous or only the basal segment dark, or at least with 1 segment dark besides the basal 3
2. Wings black; legs completely reddish yellow beyond the trochanters; first 2 abdominal segments completely rufous. Chile. *semirufus* n. sp.
2. Wings hyaline before basal veins and beyond cubital cells, the space in between a dark brown; the first 2 segment of abdomen mostly black beneath. Brazil. *braziliensis* n. sp.
3. Abdomen wholly rufous, or only basal segment dark 4
3. Abdomen with at least 1 segment black besides the basal 6
4. Legs including coxae rufous. Paraguay. *fratellus* Holmberg
4. Coxae and trochanters black or all the legs black 5
5. Coxae and trochanters black, rest of legs rufous; wings banded. Colombia. *rufigaster* Banks
5. Legs wholly black; basal abdominal segment partly black; wings nearly evenly dark. Ecuador. *loranthe* Banks
6. Abdomen yellowish on first and second segments; venter partly pale 7
6. Abdomen black on all segments 9
7. Pronotum yellowish on hind border 8
7. Pronotum not yellowish behind; legs black, except hind femora and tibiae are rufous. Argentina, Brazil. *australis* Holmberg
8. Legs yellowish except on last 1 or 2 tarsal joints, which are black; no black on second segment. Colombia. *huitaca* Banks
8. Legs yellowish except front femora and tibiae and bases of mid and hind femora which are black; black spot on second segment above; wings nearly evenly fumose. Ecuador. *quitus* Banks
9. Mid and hind femora rufous, remainder mostly black 10
9. If mid and hind femora rufous, rest of legs also 12
10. Mid and hind coxae and trochanters rufous; fore wings nearly evenly dark. Ecuador. *andicolus* Banks
10. Mid and hind coxae and trochanters black; wings hyaline with or without black bands 11
11. Wings hyaline but with two dark bands, one over the basal veins and the other over the marginal, cubital and third discoidal cells; abdomen entirely black; posterior border of pronotum very slightly angulate *jocaste* Banks
11. Wings hyaline (with brownish tint), without dark bands; tergites 1-6 on abdomen with the posterior border reddish; all of exposed tergite 7 is reddish; posterior border of pronotum transverse; all of fore femora (except

- knees), about basal half of midfemora and base of posterior femora dark; all tibiae and tarsi rufous. Brazil. *fuscus* n. sp. 13
12. Fore wings with 2 dark bands 13
12. Fore wing not banded or wholly dark 15
13. Strongly silvery sericeous on clypeus, face, mesopleura, a band across apex of propodeum, on sides of all tergites after the first, the dorsal sides of second, third and fifth tergites and across apex of fourth tergite; a few long conspicuous hairs in middle of posterior edge of sternites 2 through 6; last tergite strongly hairy. Peru *ornatus* n. sp. 14
13. No strong silvery pubescence (as glistening spots or streaks) as noted above, nor long hairs 14
14. Clypeus not $3\times$ as broad above as long in middle; frontal groove distinct only below. Colombia, Brazil. *pretiosus* Fox
14. Clypeus $3\times$ as broad as long, frontal groove complete. Colombia, Brazil, Ecuador. *machetes* Kohl
15. Fore wings without large black spot; hind margin of abdominal segments often rufous. Brazil. *marginatus* Banks
15. Fore wings with a large black spot 16
16. Legs all rufous except coxae, trochanters and last 4 tarsal joints; both pair wings all black. Argentina. *anthracinus* n. sp.
16. Legs not rufous as above; only fore wings black or with a black spot 17
17. Only the apical margin of wings hyaline, rest black. Ecuador. *orejones* Banks
17. Basal fourth of basal cell and behind it hyaline, rest black. Brazil. *nubilis* Fox

Males

1. At least the fore and mid femora partly rufous, or the legs largely pale yellowish to white; abdomen with basal 3 segments reddish or whitish, or the second segment and part of third rufous above and below; posterior border of pronotum white; last tergite white 2
1. Legs wholly black with tarsal joints sometimes dark brown; 3 basal segments of abdomen black or with sides of first and second slightly yellowish 4
2. All trochanters, femora and tarsi reddish, except the apex of posterior pair are dark at apex; first pair coxae black at base, reddish on apical half above with a white spot at apex above; last 2 pair coxae completely reddish; last joint fore tarsi black, first 4 joints yellowish, second pair tarsi with first 4 joints brown with yellow tips, last joint black; last pair tarsi all dark brown to black; fore spurs yellow, last 2 pair pure white; first 3 segments of abdomen reddish above and below, except most of dorsum of first segment, base of first segment and apex of third segment are blackish; wings clear hyaline; clypeus white with a black spot lengthwise in middle (0.2 of width). Brazil. (Fig. 5) *ruficrus* n. sp.
2. Legs pale yellowish to white, but posterior trochanters black, or only front and mid femora partly rufous 3
3. First, second and part of third segment of abdomen whitish, rest of abdomen black except for apical white spot; extreme base of first segment black; legs yellowish to white, hind trochanters black; clypeus and mandibles, except tip white; a white spot on lower lobe of pronotum just above fore coxae; last two tarsal joints of fore legs dark. British Guiana, Colombia. (Fig. 9) *modestus* Smith

3. Abdomen with first segment black (partly rufous below) second and part of third rufous above and below; legs mostly dark; front coxae pale yellowish at tips, front and mid femora rufous on apical half; front tibiae and tarsi (except last 2 joints) rufous; mid tibiae rufous on more than basal half, dark at tip, last 2 pair tarsi pale, tips of joints black, and last joint all black; hind legs almost entirely brown beyond the black coxae; tibial spurs whitish; no cloud in fore wing. Colombia. (Fig. 10) *rufigaster* Banks
4. A cloud over marginal cell extending backward across second and third cubital cells and into the discoidal cell; a very faint cloud over basal veins; clypeus almost all white, only a central triangular black spot, narrow at apex, the white spots covering about 0.8 preapical edge, and at the base the black spot occupies about 0.5 of width of clypeus; a narrow blackish, hairless rim across front of clypeus; genitalia characteristic; parameres scalloped on inner edge, with 3 transverse ridges, the apical 2 forming a U-shaped ridge; the tooth on middle of inside edge of volsellae obsolete; the outside surface of apex of volsellae with numerous small spines. Brazil. (Fig. 6) *unifascias* n. sp.
4. Wings almost hyaline or completely dark, no cloud; a narrow apical black hairless rim across front of clypeus 5
5. Wings hyaline slightly brownish; clypeus with a white spot each side covering 0.4 width of clypeus; posterior edge of pronotum with a white band; body and legs with a brownish tinge; a white ring around base of posterior tibiae; spurs white; genitalia characteristic; parameres very broad and with long hairs on all inside edge and over apical 0.25 of surface; volsellae with exceptionally large apex with blunt tip, the tooth on middle of inside very small; subgenital plate short and broad, rectangular. Brazil. (Fig. 7) *anomalus* n. sp.
5. Wings black; two white bands across the front of clypeus just back of narrow hairless rim, which do not quite touch in middle, covering about 0.25 of length of clypeus; pronotum completely coal black as is the whole body except the two white bands on clypeus; spurs black; subgenital plate characteristic; sides of basal half subparallel (slightly concave just above base), the plate becoming narrower from middle to the broad (about 0.3 as broad as base) apex, plate not rectangular as is the case in almost all other species; parameres not scalloped on outside; volsellae with a broad tooth in middle and with a very broad apex. Chile. (Fig. 8) *chilensis* n. sp.

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Growth of Green Algae with Myxomycete Plasmodia¹

WALDO R. LAZO²

ABSTRACT: Myxomycete plasmodia of several species, previously freed from bacterial contaminants, were grown on oat agar. To them were added pure cultures of 10 spp. of green algae. Three species of *Chlorella* were able to enter into full associations with *Physarum didermoides* and *Fuligo cinerea*, forming green plasmodia in which the algae multiplied in light.

Although many attempts have been made to grow myxomycete plasmodia when freed from bacteria, only a few have been successful (Cohen, 1939 and 1941; Hok, 1954; Sobels, 1950). Since 1958 I have successfully grown plasmodia under such conditions (Lazo, 1960). It has been demonstrated that most plasmodia grow slowly and with difficulty in this condition, although the plasmodium of *Physarum polycephalum* is a notable exception to this general rule. Since many plasmodia occur in nature in close association with algae, it was thought that algae might possibly serve the same purpose as do bacteria in 2-membered cultures.

MATERIAL AND METHODS

The plasmodia were grown on sterile oat agar consisting of oat flakes covered with non-nutrient agar to hold the flakes in place. They were freed from bacteria by various methods (antibiotics, low pH in the culture medium, migration). The sterility was thoroughly checked by seeding pieces of plasmodia in A-C Difco broth, brain-heart infusion, peptone-glucose broth, A-C agar, brain-heart agar. The plasmodia samples that were tested were taken, not from the advancing fronts of the plasmodia, which are almost always free from bacteria, but from immediately above the oats because this gives the best conditions for the growth of possible contaminants. The samples were seeded in the broth tubes and kept in the incubator at 25° C for ten days. Then, a sample of this broth was seeded in agar plates and again in broth tubes and kept in the incubator for an additional ten days.

The bacterium-free plasmodia were grown in pure 1.5 per cent agar and oats at a temperature of 25° C.

¹ This study was carried out at the Dept. of Biology of Princeton University and at the Dept. of Botany of the State University of Iowa. I wish to express my gratitude to Dr. J. T. Bonner, Dr. C. J. Alexopoulos, Dr. F. H. Johnson, Dr. Luigi Provasoli who kindly supplied me with the algae that I used in this experiment, Mr. O. R. Collins and Mr. J. Koevenig who kindly supplied me with the fruiting bodies of some of the Myxomycetes that I used and I especially acknowledge the invaluable counsel and help of Dr. G. W. Martin in the preparation of this manuscript.

This work was done on a Rockefeller Foundation fellowship, which is gratefully acknowledged, while on leave of absence from the University of Chile.

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The plasmodia used were those of *Physarum didermoides*, *P. polycephalum*, *P. gyrosum*, *Fuligo septica*, *F. cinerea*. Later some plasmodia were used that were contaminated with bacteria: *P. pusillum*, *P. compressum*, *Didymium iridis*, *D. squamulosum*, *D. minus*.

The algae used were *Euglena gracilis*, *Chlorella paramoecium*, *C. protothecoides*, *C. xanthella*, *C. saccharophyla*, *C. vulgaris* 259, *C. pyrenoidosa*, *C. luteo-viridis*, *C. zopfingiensis*, *C. ellipsoidea*, all in pure culture.

The plasmodia were seeded in the oat-agar plates and allowed to grow for three to five days. Then a small portion of each plasmodium was inoculated with one drop of the algal cells on the surface of the plasmodium. After inoculation the culture plates were placed in the incubator under fluorescent lamps at a constant temperature of 25° C.

RESULTS

The algae were incorporated in the bacterium-free plasmodia of *P. didermoides* and of *F. cinerea* in several trials, but were not successfully incorporated in those of any other species. All but one of the plasmodia which had not been freed from bacteria failed to incorporate the algae; the exception was *P. didermoides*. The bacterium-free plasmodia of *P. polycephalum*, *P. gyrosum* and *F. septica* appear to take the algal cells and digest them, but the plasmodia do not become green. On the other hand, after three or four days the white plasmodia of *P. didermoides* and *F. cinerea* appeared green in color and under a microscope the algal cells could be seen moving with the protoplasm within the plasmodial veins. Later, the algae were deposited in the walls of the veins and, with the walls, formed a green crust which, when the plasmodium became old and dried, usually cracked. The veins then appeared dry and white.

Summarizing these results, of the species of algae tested only three, *C. protothecoides*, *C. xanthella*, and *C. ellipsoidea*, were able to enter into full association with two species of myxomycetes tested, *P. didermoides* and *F. cinerea*. There was, in addition, some slight evidence of temporary association between these species and *C. saccharophyla* and *P. didermoides*, but it failed to persist.

Results were negative in all trials with *P. polycephalum*, *P. gyrosum*, *P. pusillum*, *P. compressum*, *F. septica*, *D. iridis*, *D. minus* and *D. squamulosum*.

If transfers are made from a green section of the plasmodium the new plasmodia will be green also. A green plasmodium may even be obtained from a white one, provided the white one has a few algal cells but an insufficient number to make it appear green at the time of the transfer. On the other hand, if a green plasmodium is kept in darkness, one part of it may become white if in the migration process that part loses all the algae.

The association plasmodium-algae grows much better than the plasmodium alone and is much more resistant to acidity than is the plasmodium in pure culture. *P. didermoides* and *F. cinerea* associated

with *C. protothecoides* or *C. xanthella* were able to grow in a medium buffered at pH 4.5 (McIlrairie, 1921). In both cases the plasmodia without algae grew only slightly or not at all at that pH.

Myxomycetes which have been purified from bacteria are rarely able to fruit. *Physarum polycephalum* is exceptional in this respect, as in many others. However, by the use of streptomycin I obtained a strain of *P. polycephalum* that never fruited unless it became contaminated. In the case of *F. cinerea* and *Chlorella*, fruiting can be obtained in about two or three weeks. The control plates do not fruit.

The bacterium-free plasmodia of *P. didermoides* do not fruit either associated with algae or alone.

The spores of *F. cinerea*, even when many appear abnormal, are viable; I have obtained plasmodia from them on a few occasions in bacterium-free condition. Algal cells were present.

DISCUSSION

It is premature to say that a symbiosis has been obtained. It does seem that some algae may function in the same way as do bacteria with some of the Myxomycetes, and in the case of *F. cinerea* they may help the fruiting process. It is not yet clear why the algae can grow on the membranes of some plasmodia and not on those of others.

Pinoy (1907) and Skupiński (1928) postulated that Myxomycetes could be considered as symbiotic organisms with bacteria. It is now clear that bacteria, at least, not only make possible the vegetative growth of the plasmodia, but even contribute to completion of the life cycle. The results here reported seem to demonstrate that some algae may replace bacteria, functioning in the same way.

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Fishes of Chincoteague and Sinepuxent Bays¹

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ABSTRACT: A comprehensive monthly trawl survey of Maryland and Virginia's Sinepuxent and Chincoteague Bays found 65 species of fishes within 40 families and 59 genera currently occupying these two seaside bays. Twenty-three species were new to the fauna which, since 1876, now totals 99 species. Various methods, beach seining, crab potting, hook and line fishing and wire oyster test trays, were employed to capture smaller species. An annotated list of species, as well as comments regarding seasonal population dynamics, size ranges, ecological requirements or preferences, are presented. Fish distributions, hydrographic conditions and invertebrates, mainly crabs, squids and *Aurelia* illustrate the predominant use of the southern inlet as an avenue of entry into these bays. The establishment of the newer northern inlet at Ocean City, Maryland, has had a profound influence on the hydrography of Sinepuxent Bay. This has resulted in extinction, entry or reduction of various fish species. Little use is made of the northern inlet as an avenue of entry into Chincoteague Bay. The fishes and crabs that do enter Sinepuxent Bay by way of the northern inlet are currently not found beyond the 5-8 mile southward influx of water from that inlet.

The permanent establishment of the present northern inlet to Chincoteague Bay, via Sinepuxent Bay, in 1933 (Md. Cons. Dept. 1933) along with the economic development of the Ocean City, Maryland area places a greater demand on the need for increased knowledge of the fishes of this area and the effects of these inlets on species abundance, presence or distribution. Although Giovanni da Verazzano accidentally sailed into Chincoteague Bay in 1524 (Covington, 1915), it was not until 1876 (Uhler and Lugger, 1876) that the first contribution of 12 species of fishes was collected from these waters (Fig. 1). Seven additions to this list of fishes were made by Lugger (1877, 1878) who sampled the southern inlet at Chincoteague, Virginia. Goode and Bean (1879) added two more species to the list. Fowler (1913-45) in a series of nine papers and sporadic surveys, primarily at Chincoteague and Franklin City, Virginia, and Ocean City, Maryland, listed 51 additional species to extend the total to 72 then known from Sinepuxent and Chincoteague Bays, Maryland and Virginia, and their inlets (Table III). Murphy (1960) recorded three commercial species in the early catch records of these bays. Arve (1960) trap netting in Chincoteague Bay, north of South Robin Marsh, recently added two species to the list of fishes known previous to 1959. Dillon (1960) notes the sport fishery and species about Ocean City, Maryland. No comprehensive study of the fishes or their distribution and seasonal abundance within the entire length of the bays has ever been attempted.

¹ Contribution No. 161, Maryland Department of Research and Education, Solomons, Maryland.

Acknowledgments.—It is a pleasure to acknowledge the generous assistance of the following people who helped in various ways toward successful completion of this project: Messrs. Fred Sieling and John Arve of the Chincoteague Bay Station of the Maryland Department of Research and Education for facilities, boat use and physical endurance beyond the call of duty; Mr. Thomas Carver, U. S. Fish and Wildlife Service Laboratory at Franklin City, Virginia, for use of the R. V. "Louise"; Mr. George Ward, for piloting the "Louise" and Messrs. Michael Castagne and George Griffith for specimen information around the Franklin City Laboratory and lower Chincoteague Bay region; Mr. N. Jester of the Pocomoke High School for use of his data concerning odd and rare specimens which he obtained from the lower bay area; Messrs. H. Schwartz and John Edgar of Antioch College, Ohio; Mr. C. Huckins of the Chesapeake Biological Laboratory; Mr. W. Meredith of Mt. St. Mary's College, Emmitsburg, Maryland, all of whom contributed field work; Dr. Ernest A. Lachner, Associate Curator Fishes, U. S. National Museum, for his critical review of the manuscript and suggestions regarding presentation and format; Messrs. G. F. Beaven, D. G. Cargo, H. J. Elser and J. R. Longwell of the Chesapeake Biological Staff for additional grammatical and constructional comments; and Mrs. G. Lankford for typing the final draft of this paper.

DESCRIPTION OF SINEPUXENT AND CHINCOTEAGUE BAYS

The study area of Sinepuxent and Chincoteague Bays is located in Worcester County, Maryland, and Accomack County, Virginia. The combined length of these continuous bays is some 28 miles and lies in a NE-SW direction between the latitudes $38^{\circ}20'$ - $37^{\circ}53'N$ and longitudes $75^{\circ}06'$ - $75^{\circ}27'W$. The bays are separated from the Atlantic Ocean by a narrow strip of land, Assateague Island (Fig. 1). One natural inlet, with several smaller inlets, exists at the southern end at Chincoteague, Virginia. A hurricane-cut inlet is maintained (since 1933) at the northern end at Ocean City, Maryland. The maximum width, about 5 miles, is in Chincoteague Bay near Public Landing, Maryland. The narrowest area, one-quarter

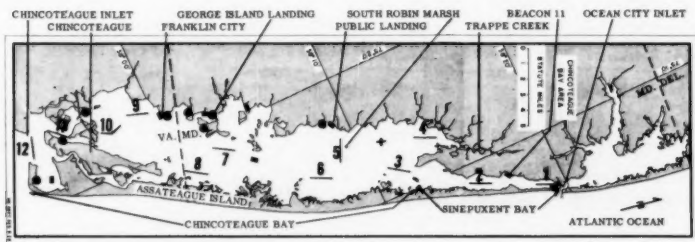


Fig. 1.—Location of trawl (numbers), beach seine (dots), oyster tray (bars), and wire trap (cross) stations in Chincoteague and Sinepuxent Bays, Maryland and Virginia. 1. Beacon 4, Sinepuxent. 2. Beacon 17, Sinepuxent. 3. Beacon 35, Sinepuxent. 4. Newport Bay. 5. South Robin Marsh. 6. Foxhill levels. 7. White Rock. 8. Cedar Islands. 9. Franklin City. 10. Beacon 10, Virginia. 11. Beacon 7, Virginia. 12. Beacon 5, Virginia.

of a mile or less, exists in the 9 mile Sinepuxent Bay, the northernmost of the two bays. The watershed of the study area is 127.4 square miles while the area of the bay is 115.2 square miles (Bailey; personal letter; May 4, 1960). The largest freshwater tributary is Trappe Creek which enters the Newport-long Point area of the northern end of Chincoteague Bay. The average depth of both bays is 4 feet with the greatest depths of 25 and 50 feet occurring in channels at either inlet. The area is subject to constant wave action, particularly during the summer, for winds sweep freely over the adjoining dune or marsh shores. Turbidity is high. The shallowness permits abundant growths of bryozoans, *Ulva* and the red algae, *Agardhiella tenera*. Rainfall in the area amounts to about 48 inches per year (Sieling, 1960). The salinity patterns are well documented (McGary and Sieling, 1953, Md. Cons. Dept., 1934; Sieling, 1955, 1958; Sieling and McGary, 1952) and generally range from 13 to 30 o/oo (maximum 38 o/oo) at Public Landing, Maryland, and 22 to 36 o/oo at Franklin City, Virginia, with higher readings usually being noted at either inlet (Table I). Bottom salinities are approximately the same as surface salinities (Table II) throughout the area. Evaporation is highest during summer months (Pritchard, 1960). Tidal amplitude

TABLE I.—Surface and bottom salinities at 12 trawl stations, 1959, in Sinepuxent and Chincoteague bays

Sta- tion*		M O N T H							
		Apt	May	Jun.	Jul.	Aug	Sep	Oct.	Dec.
1	S	30.2	29.8	31.1	31.8	31.2	30.8	29.7	30.8
	B	29.9	31.1	31.6	31.6	30.7	29.3
2	S	30.7	28.8	30.4	31.5	31.2	30.8	29.5	27.1
	B	28.6	31.0	31.5	31.6	31.1	29.1
3	S	26.0	26.4	30.4	33.2	25.6	29.8	28.6	27.3
	B	26.4	30.2	33.3	25.5	29.7	28.6
4	S	24.6	24.0	26.7	30.2	22.7	27.3	28.1
	B	24.0	28.5	30.2	22.9	27.1	28.0
5	S	27.2	25.4	28.4	30.7	24.2	29.0	29.9	28.4
	B	25.9	28.4	31.1	24.7	28.9	29.9
6	S	26.0	26.1	29.9	32.3	25.1	29.0	29.7
	B	26.3	30.0	32.5	25.5	28.9	29.5
7	S	28.1	26.9	32.0	33.7	29.3	31.1	30.3	28.8
	B	26.5	33.0	33.7	28.8	31.2	30.6
8	S	28.4	28.9	32.3	33.8	28.2	30.4	30.6
	B	28.6	33.2	33.7	28.8	31.2	30.6
9	S	29.1	29.5	30.7	32.7	30.0	32.1	30.0	29.1
	B	28.8	31.1	32.3	30.2	31.8	30.3
10	S	30.6	29.9	31.9	32.1	31.9	31.1	31.1	29.1
	B	29.9	32.7	32.0	31.8	31.2	31.4
11	S	31.9	31.0	31.5	32.0	32.0	31.6	30.0	31.4
	B	31.2	31.6	31.8	32.0	31.6	30.6
12	S	31.0	31.1	32.1	32.3	31.9	31.8	29.9	31.4
	B

* As in Figure 1. S = Surface; B = Bottom.

at Ocean City averages about 3.5 feet and at the Chincoteague Inlet about 4.0 feet. Water temperatures average 25-27°C in the summer throughout the central portion of the study area and 23-24° at the inlets, which are influenced by oceanic waters (Table II). Pritchard (1960) estimates 9.3 days for 50 per cent of the water to be renewed while 62 days are needed for a 99 per cent water renewal. Short periods of complete ice cover and -1.7°C water temperatures have been recorded. The bottom types and locations are documented by

TABLE II.—Air, surface and bottom water temperatures at 12 trawl stations 1959, in Sinepuxent and Chincoteague bays

Sta- tions*		M O N T H							
		Apr	May	Jun.	Jul.	Aug	Sep.	Oct.	Dec.
1	S	6.0	17.4	20.2	26.5	20.3	28.0	14.0	8.0
	B	17.2	20.0	26.8	20.0	28.5	15.0
	A	15.0	26.3	20.2	20.5	11.0	10.0
2	S	9.2	17.9	28.0	21.0	23.0	14.0	5.5
	B	17.4	28.0	21.0	23.0	15.0
	A	17.9	**	26.8	21.0	22.0	10.0	7.0
3	S	10.4	20.0	**	26.7	24.0	23.5	14.0	6.0
	B	17.8	**	26.7	24.0	23.2	13.2
	A	16.1	**	24.0	22.5	22.0	10.0	6.7
4	S	9.2	18.0	22.2	26.7	24.3	23.8	14.0
	B	17.8	22.2	26.6	23.0	23.2	13.5
	A	15.0	22.8	24.0	22.0	20.0	8.0
5	S	9.4	17.8	21.9	25.8	26.9	24.0	12.5	6.3
	B	18.9	22.2	26.0	26.5	23.2	13.2
	A	15.0	19.4	22.5	29.5	20.0	8.0	6.3
6	S	9.8	20.0	26.6	26.6	22.0	13.0
	B	18.9	26.5	26.5	23.0	12.5
	A	18.0	24.0	27.5	19.0	8.0
7	S	10.6	17.9	22.0	27.3	26.5	21.0	12.0	6.2
	B	17.8	22.0	27.3	26.0	20.0	12.4
	A	14.4	22.0	25.0	27.0	16.0	9.6	13.0
8	S	10.4	17.7	22.8	26.9	26.0	20.5	11.6
	B	17.8	22.6	26.9	26.0	20.0	11.7
	A	16.1	20.0	25.0	27.0	15.0	9.0
9	S	11.0	18.9	23.3	25.0	25.4	22.1	12.1	14.9
	B	18.6	22.4	28.0	25.4	22.0	13.7	6.6
	A	16.7	22.8	29.0	24.0	22.1	14.5
10	S	10.6	19.1	23.0	28.8	24.8	21.0	13.0	14.9
	B	19.1	23.2	28.3	24.6	21.0	12.6	6.6
	A	23.0	28.0	24.0	23.2	11.8
11	S	9.8	18.7	26.0	23.7	22.4	12.7	7.6
	B	18.9	26.0	23.5	22.8	12.6
	A	27.1	25.0	20.0	11.6	14.0
12	S	9.8	18.3	25.8	23.6	22.8	12.9	8.0
	B
	A	25.3	24.0	22.5	11.4	12.0

* As in Figure 1. S = Surface; B = Bottom; A = Air; = No data;

** = Thermometer broken.

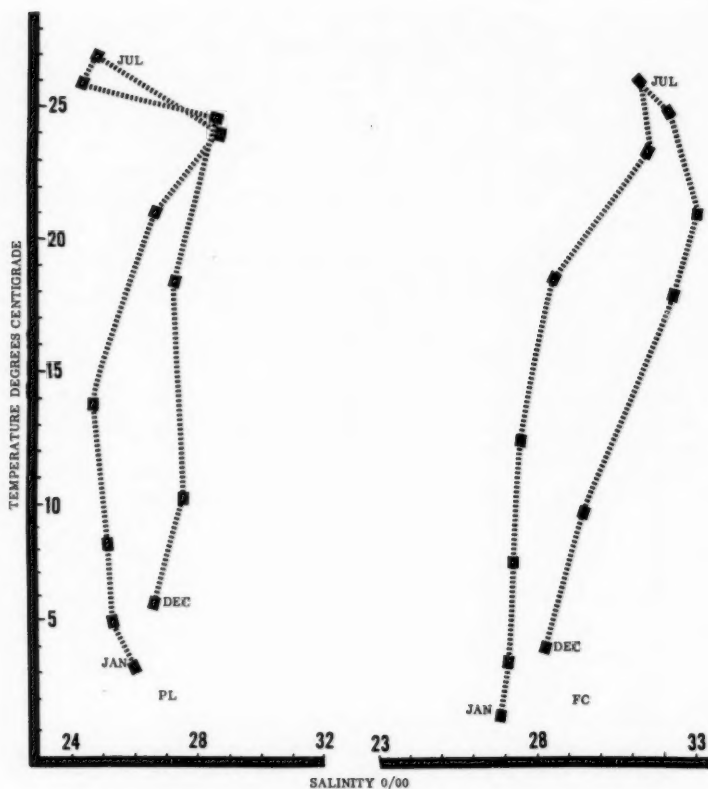


Fig. 2.—Hydroclimatographs for Public Landing (PL), Maryland and Franklin City (FC), Virginia.

U. S. Geological Survey (1937), Stout (1953) and Wells (1957). Generally sandy shoals exist on the eastern side of the bay while clay-mud bottoms predominate in the deeper western portion.

METHODS

Collections and records appearing herein were made during the period March 30 to December 16, 1959. Observations made between 1957-1960 from other localities are also included.

The primary collecting gear was a 25-foot otter trawl. Data from beach seining in the lower Virginia portion of Chincoteague Bay were obtained with a 50-foot, one-quarter-inch bag seine. Benthic species were captured in trays containing oysters which were set throughout the entire western length of Sinepuxent and Chincoteague Bays.

Seguin (1960) obtained data on young *Cynoscion regalis* with a small 15-foot tri-net off South Robin Marsh (Station 5). Verified specimens captured by hook and line have also been included.

Twelve monthly stations were established. The collecting effort at a station consisted of 15-minute tows (usually north to south) with the wind to facilitate easier boat handling. These tows in Sinepuxent Bay were along the channel which ran in a general north-south direction. The remaining stations were established on east-west lines five miles north of each other (Fig. 1). The latter stations encompassed deep channels and shoals over all types of bottoms. Some bias entered into the final placement of some of the easterly stations because of impenetrable shoals and boat draft, however, this was minimized as much as possible.

All specimens, unless stated otherwise, were measured to total length and released. Flounders, sharks and sea bass were tagged with monel strap tags on the left opercle to obtain data on their migratory patterns upon recapture.

To facilitate the presentation of localities a system of abbreviations was devised. The abbreviations used are OC for Ocean City, Maryland; PL for Public Landing, Maryland; GIL for George Island, Landing, Maryland; FC for Franklin City, Virginia; Ch for Chincoteague, Virginia; and Co for Cockle Creek, Virginia.

ANNOTATED LIST OF FISH SPECIES

Carchariidae — Sand Shark Family

1. *Carcharias taurus* Rafinesque. Sand shark.

Several sand sharks 500-750 mm (all measurements refer to total length unless specified otherwise) were captured at OC, FC, and Ch during the summer of 1959 on baited clam or peeler blue crab, *Callinectes sapidus*. Previously reported by Fowler (1927) at Ch.

Carcharhinidae — Requiem Shark Family

2. *Mustelus canis* (Mitchill). Smooth dogfish.

Two males, 900 and 1100 mm, were caught by hook and line at FC, July 29, 1958. Small specimens taken at Ch by Fowler (1913, 1927, 1930).

3. *Carcharhinus milberti* (Müller and Henle). Brown shark, Sandbar shark.

This species is only tentatively included for there are numerous sightings and reports of six-foot sharks within the bays. Sightings have been in Sinepuxent Bay (Station 6) and at Ch. Fowler captured small brown sharks at Ch (1927, 1930) and Co (1930).

Squalidae — Spiny Dogfish Family

4. *Squalus acanthias* Linnaeus. Spiny dogfish.

Four fish, two of each sex, males 800, 880 mm, females 755, 770 mm, were taken by trawl at Station 1 near OC on March 31,

1959. Undoubtedly this species ranges some distance from each inlet into the two bays proper; however, no others were captured or have been reported previously.

Rajidae — Skate Family

5. *Raja eglanteria* Bosc. Clearnose skate.

Eleven individuals, all from Station 12 were captured May 9, 1959; 2 males and 7 females (1000-1500 mm wide), June 1, one male (1180 mm wide), and October 1, one female (1360 mm wide). This species is present in oceanic shoal waters from May to November after which it moves into deeper waters outside of the bays. Apparently this species doesn't move far beyond the inlets into Chincoteague or Sinepuxent Bay proper. Several individuals have been taken by hook and line at the northern inlet. Two frayed egg cases were found floating near Foxhill Levels (Station 6). Clusters of egg cases of this species were brought up in the trawl as far south in Sinepuxent Bay as Station 2. *R. eglanteria* was previously reported abundant at Ch (Fowler, 1914, 1927, 1930) and Co (Fowler, 1914, 1927).

Dasyatidae — Stingray Family

6. *Dasyatis americana* Hildebrand and Schroeder. Southern stingray.

One female, 711 mm wide and weighing 50 pounds, was captured at FC, July 22, 1958, by Mr. Nelson Jester. Other specimens up to 3½ feet (1016 mm) wide have been sighted in Chincoteague Bay as far north as Foxhill Levels (Station 6) where they frequent the shallows and sandy bottoms on the eastern side. Occasionally a few large individuals are sighted in Sinepuxent Bay near Station 1. Arve (1960) reports one small specimen caught in a trap net just north of South Robin Marsh (Station 5).

7. *Gymnura micrura* (Bloch and Schneider). Smooth butterfly ray.

A pregnant female, 798 mm (31¾ inches) wide, with three male embryos, was captured at Station 12, September 17, 1959. The left uterus possessed one embryo (235 mm wide) while the right possessed two embryos (230 mm wide) whose snouts and wings were curved and folded inward on each other as noted by Radcliff (1916). These embryos are larger than the 5-6 inch specimens noted for a nearly full-term *micrura* (Radcliff, 1916; Smith, 1907) and a little larger than those noted by Bigelow and Schroeder (1953). Umbilical scars were obliterated. The lack of tail spine, large size and spotting around the edge of the wings of this specimen were distinct. These characters are within the size and range of variations noted by Bigelow and Schroeder (1953).

Myliobatidae — Eagle Ray Family

8. *Rhinoptera bonasus* (Mitchill). Cownose ray.

This species was not captured during the present survey, but

is present in Chincoteague Bay from June 2-October 15. It frequents the Chincoteague, Virginia area in large schools and is detested by the oyster planters of that area. This ray, up to 3 feet wide, is accused of the destruction of huge, if not entire, beds of oysters, seed oysters and clams. Many and varied devices are built around these beds but give little if any protection. It is my belief that the principal culprit is a dasyatid rather than *R. bonasus*. Cow-nose rays, locally called "bullfish," have been sighted as far north as Public Landing (near Station 5), Maryland. No cow-nosed rays seem to enter Sinepuxent Bay via the northern inlet.

Clupeidae — Herring Family

9. *Clupea harengus harengus* Linnaeus. Atlantic herring.

One 245 mm Atlantic herring was taken at Station 3 near South Point April 1, 1959. A short term anchor gill net fishery exists for this species between Stations 4-6. Apparently the Atlantic herring enter Chincoteague Bay during their northerly migrations and then exit, perhaps via the Ocean City inlet. Luger (1877) noted large schools in Chincoteague Bay.

10. *Alosa sapidissima* (Wilson). American shad.

Although Fowler (1913) noted the presence of this fish in the pound nets around the lower inlet, only one 352 mm male shad was captured at Station 11, April 1, 1959. Some shad may stray into the Chincoteague, Virginia, inlet on their annual northerly spring migrations to spawn. None, however, have been recently known from the bay north of Station 11 where they contribute to the pound net fishery near Ch. Apparently, based on catch records for the period 1890-1908 (Murphy, 1960), sizable spawning runs utilized the fresher upper portions and bays above Ocean City prior to the opening of inlets which permitted salt water to enter the formerly fresh water areas. Few if any local spawning areas remain.

11. *Brevoortia tyrannus* (Latrobe). Atlantic menhaden.

Individuals varying in length from 48 to 107 mm of this pelagic species are common throughout Chincoteague Bay. Concentrated schools occur in June and July. Stations 4 and 5 consistently yielded samples. Fowler (1913, 1914, 1927, 1930) noted the abundance of menhaden about the southern inlet while Arve (1960) reports some caught in trap nets north of Station 5.

Engraulidae — Anchovy Family

12. *Anchoa mitchilli mitchilli* (Valenciennes). Bay anchovy.

The anchovy, 77-92 mm in length, is the most abundant summer species throughout Sinepuxent and Chincoteague Bays. Greatest concentrations of anchovies occurred in the vicinity of each inlet. This species was most common in both bays during October. Larval anchovies were common in the central portion of the study area around Stations 4-8 between April-May and October-December. Fowler (1913) observed some specimens on Assateague Island, apparently in an overflow tide pond.

13. *Anchoa hepsetus hepsetus* (Linnaeus). Striped anchovy.

The striped anchovy was found sporadically in Sinepuxent Bay, Stations 1-4, in August. Specimens varying in length from 77 to 137 mm were captured. Heavy external parasitization by a copepod, *Lerneaeenicus radiatus*, was common.

Synodontidae — Lizardfish Family

14. *Synodus foetens* (Linnaeus). Inshore lizardfish.

Four individuals, 77-98 mm, of this southern species were captured in August and September at Stations 10 and 11. High water temperatures and high salinities during this period most likely influenced its presence. A number of lizardfish were taken during 1957, 1959, and 1960 in Chesapeake Bay as far north as Chesapeake Beach, Maryland.

Anquillidae — Eel Family

15. *Anquilla rostrata* (LeSueur). American eel.

Three eels were captured in April, June and July at Stations 3, 4, and 5, respectively. This species frequents both bays until September as it is taken in crab pots during that period. Mr. N. Jester obtained a specimen from Co, June 30, 1958. Specimens are known from Ch (Fowler, 1914, 1927) and near Station 5 (Arve, 1960).

Belonidae — Needlefish Family

16. *Strongylura marina* (Walbaum). Atlantic needlefish.

One sight record of this species was obtained during the study period. The fish, about 16 inches long, were seen swimming along the surface of Chincoteague Bay, south of PL. Mr. M. Castagne captured a specimen 20¾ inches long at FC in 1958. Fowler (1913) reported this species at FC and OC (Fowler, 1919).

Cyprinodontidae — Killifish Family

17. *Cyprinodon variegatus* Lacépède. Sheepshead minnow.

Schools of 30-36 mm adults were captured along the PL beach. This species occurs along all beaches throughout the two bays. Fowler (1913) noted it at Ch as well as in Sinepuxent Bay (1918).

18. *Fundulus heteroclitus macrolepidotus* (Walbaum). Mummichog, Bull minnow.

The most common cyprinodontid throughout the bays. Huge schools are found along the beaches and especially around the docks at OC, PL, GIL, FC and Ch. Previously noted by Fowler (1913) at Ch, OC and in Sinepuxent Bay (1918).

19. *Fundulus luciae* (Baird). Spotfin killifish.

A single fish (56 mm) was seined near FC July 22, 1958, by Mr. N. Jester. Others have been seined north in Chincoteague Bay to Purnell Point. Fowler (1913) noted *luciae* in freshwater pools at Ch, but not in the bay proper.

20. *Fundulus majalis* (Walbaum). Striped killifish.

Large schools of this killifish inhabit the beaches throughout the southern portion of Chincoteague Bay south of GIL. Fowler (1913) recorded specimens at Ch and in Sinepuxent Bay (1918).

Gadidae — Cod Family

21. *Gadus morhua* Linnaeus. Atlantic cod.

Five- to seven-pound cod were caught in commercial fish pots from FC south during April 1-7, 1960. These were part of a large school of fish which remained inshore along Assateague Island all winter and contributed heavily to a gill net and hook and line sport fishery. None have been previously reported or caught in the bays. None are known to have entered via the northern inlet at OC.

22. *Merluccius bilinearis* (Mitchill). Silver hake, Whiting.

The whiting is found from September to May near the Chincoteague, Virginia, inlet. Schools of whittings occur offshore near the Ocean City inlet but they do not seem to enter Sinepuxent Bay via that inlet. The young (90-160 mm) enter Chincoteague Bay and move north to Long Point and Station 10 as stragglers. Adults were always found at Stations 11 and 12.

23. *Urophycis regius* (Walbaum). Spotted hake.

The spotted hake is present in the upper one-third of Chincoteague Bay, mainly between Stations 4-6, and Sinepuxent Bay, December to June as yearlings 68-92 mm and during April to June as 100-167 mm subadults. Small young may be found from May to November at Station 12 in the southern inlet. Larger specimens, above 170 mm standard length, are obtained outside the bays by the offshore trawlers. However, *U. chuss* is more common offshore than *regius* and the former constitutes a greater part of the trawl fishery catch (Murphy, 1960). *U. chuss* has yet to be found in either bay.

Syngnathidae — Pipefish Family

24. *Hippocampus erectus hudsonius* DeKay. Northern spotted seahorse.

Although not taken during the May, June or December samples, this subspecies (Briggs, 1958) is common along each inlet, especially at Stations 1-4 and 10-12. Specimens varying in total length from 58 to 150 mm were usually found clinging to the red algae *Agardhiella tenera* which abounds in the inlets and in the other portions of Chincoteague Bay. Uhler and Lugger (1876) noted seahorses in Sinepuxent Bay. Many are caught annually by tourists and trawlers in and around Ocean City and the offshore waters. Nomenclatorially Briggs (1958) is followed instead of Ginsburg (1937). Ginsburg (1937) did not apply the name of *erectus* (Perry, 1810), to this northern form.

25. *Syngnathus floridae* (Jordan and Gilbert). Dusky pipefish.

The first (118 mm) of two fish recorded from Chincoteague Bay was caught at White Rock (Station 7) while the other (125 mm) was taken at Beacon 10, Virginia (Station 10).

26. *Syngnathus fuscus* Storer. Northern pipefish.

The northern pipefish was found at all stations in October and between March and May. Individuals varied from 30-192 mm. This species was absent between Stations 4-9 during the period June to September.

Serranidae — Sea Bass Family

27. *Centropristes striatus* (Linnaeus). Black sea bass.

The black sea bass is common in Chincoteague Bay from April 1 to November 5, 1959. It is confined in Sinepuxent Bay to the inlet area near Station 1, rarely straying south to Station 4. Juvenile specimens, 30-37 mm standard length, predominate the April populations. By November these fish reach a standard length between 98 and 182 mm. In April and May black sea bass, locally called blackwill, are found at both inlets, Stations 1 and 12. Throughout the summer the schools continue to move northward and southward until they occupy Chincoteague Bay from Station 4 south and Sinepuxent Bay between Station 1 and Beacon 10, seldom occurring between Beacons 10 and 35. Populations were largest during the months of August, September and October. Many were caught during this period in traps and crab pots as well as in the trawl. Tagging failed to reveal definite migration patterns. Trawl sampling was a better means of observing population dynamics. During September there was a gradual outward movement of sea bass from the area and by November only an occasional specimen could be captured just north of PL. None were found in December. Fowler (1927) noted the sea bass abundance at Ch., while Arve (1960) trap netted 288 in 1958-1959 north of Station 5.

28. *Roccus americanus* (Gmelin). White perch.

White perch were not recorded during these observations, although they have been taken in crab pots or wire fish traps. Fish traps set in 1958 and 1959 by Arve (1960), over planted oyster shell beds near Station 4 and Newport Bay, captured 78 white perch. Murphy (1960) notes the previous importance of this species to the commercial fisheries of Chincoteague Bay where it often contributed up to 77,680 pounds to the fishery before the new northern inlet was formed. Today a few pounds are caught occasionally, usually only enough for private consumption. Fowler (1913, 1914, 1927, 1930) noted this species at OC, FC and Ch.

29. *Roccus saxatilis* (Walbaum). Striped bass.

An individual approximately 10 inches long was caught by hook and line at the Franklin City, Virginia pier while several others up to four pounds in weight were caught in Swan's Gut Creek. Local

fishermen did not know this fish in the study area nor has it been caught inside the inlet or mentioned in the literature. It does occur (December 1-9, 1959) just outside the Chincoteague, Virginia inlet and constitutes an excellent gill net and sport fishery in that area during some years.

Pomatomidae — Bluefish Family

30. *Pomatomus saltatrix* (Linnaeus). Bluefish.

Two young bluefish were trawled on July 8, 1959, at Station 10 (143 mm) and Station 11 (98 mm). Two hundred and thirty-two pounds of adult bluefish were captured by commercial stake gill nets at Foxhill Levels (Station 7) in September of 1959. Fifty pounds were taken by similar gear near Station 2 in Sinepuxent Bay. Arve (1960) captured some larger specimens in traps set near Station 4. Fowler (1913) noted small specimens at FC and Ch. Schools of bluefish from offshore apparently move in and out of the bays during the summer and fall months. Little else is known of their movements.

Carangidae — Jack Family

31. *Caranx crysos* (Mitchill). Blue runner.

The blue runner is common in Chincoteague Bay from Red Beacon 10 (Station 10) south during July and August. Specimens reaching 10 inches in length are often taken. Several were kept alive in May, 1958, at the U. S. Fish and Wildlife Laboratory, Franklin City, with perhaps a specimen of *C. hippos*. However, since the latter is missing, identification could not be verified and I have not placed it in this list.

32. *Selene vomer* (Linnaeus). Lookdown.

One specimen of this southern species was captured while beach seining in Watt's Bay in the summer of 1957. The lookdown was noted from these waters by Goode and Bean in 1879.

Pomadasyidae — Grunt Family

33. *Orthopristis chrysopterus* (Linnaeus). Pigfish.

The pigfish was found approximately from the Maryland-Virginia state line south in Chincoteague Bay and was especially common around piers. Specimens up to 7 inches long are found all summer. Fowler notes pigfish at OC (1913) and in the fall at Ch (1927).

Sciaenidae — Drum or Croaker Family

34. *Bairdiella chrysura* (Lacépède). Silver perch.

The silver perch occupies both bays from May to September with greatest concentrations occurring in August and September. Juveniles are found throughout the entire area and vary from 28 to 67 mm in standard length, the adults vary up to 168 mm. In May and June an occasional adult specimen can be found as far north in Chincoteague Bay as South Robin Marsh (Station 5). Silver perch

were previously noted in Chincoteague Bay at FC and Ch by Fowler (1913).

35. *Cynoscion regalis* (Bloch and Schneider). Gray trout, Weakfish.

Young trout occur in huge schools in August and September within Sinepuxent Bay south to White Rock (Station 7). Specimens 53-190 mm standard length occur in Chincoteague Bay from White Rock south in August. Trout occur from Cedar Island (Station 8) south in September. Occasional summer schools are found as far north in Chincoteague Bay as South Robin Marsh (Station 5, Seguin 1960). Trout do not move much further south than Station 2 (Beacon 17) in Sinepuxent Bay during the summer. One hundred and eleven pounds of adult trout were caught in September by commercial gill nets in Sinepuxent Bay. Fowler (1913; 1927) found trout at FC and Ch as well as at Co (1930). Fowler (1928) reports *C. nebulosus* from OC; however, this species was not taken during this survey.

36. *Leiostomus xanthurus* Lacépède. Spot.

The spot ranks second in abundance in Chincoteague Bay. It appears in June, is most abundant in June and July, and remains until late October. Large schools appear in Sinepuxent Bay and in the upper one-half of Chincoteague Bay from Stations 1-6. This population slowly shifts southward in August and September, until in September the northern edge of this population occurs only south of George Island Light (Va. Beacon 2). During this same period a few spot can be found in Sinepuxent Bay, a mile or so south of the northern inlet. Specimens taken during early summer were young-of-the-year or slightly older, while September and October specimens were adults which ranged to 190 mm standard length. Fifty-five pounds of spot were taken in September in Sinepuxent Bay by commercial gill net. Uhler and Lugger (1876) noted spot in Sinepuxent Bay while Fowler (1927, 1930) noted them from Chincoteague Bay in the fall. Arve (1960) captured 10 spot by trap netting north of Station 5.

37. *Menticirrhus saxatilis* (Bloch and Schneider). Northern kingfish, King-whiting.

This species is present August to September in the southern portion of Chincoteague Bay and around that inlet. Specimens were rarely found north of Station 10. In October kingfish, 108-198 mm, were found at inlet Stations 1, 11 and 12. Fowler (1913, 1927, 1930) noted their presence around Ch with the farthest northern record at FC (1913).

38. *Micropogon undulatus* (Linnaeus). Atlantic croaker.

The croaker was common in 1958 from Beacon 10 (Station 10) south in Chincoteague Bay during July to September. A few stragglers have been caught as far north in this bay as South Point.

Captured croakers are usually small, 150 mm; however, an occasional specimen of 350 mm is captured.

Sparidae — Porgy Family

39. *Archosargus probatocephalus* (Walbaum). Sheephead.

Four sheephead (180-250 mm) were caught by hook and line at the Franklin City pier in November, 1959.

40. *Lagodon rhomboides* (Linnaeus). Pinfish.

Although not captured during the present survey, this species frequents Chincoteague Bay during years of exceedingly high vegetation growth. Pinfish (Arve, 1960) were abundant in Chincoteague Bay in 1958 as far north as South Robin Marsh (Station 5). A slightly cooler year with less vegetative growth apparently kept this species out of the bay in 1959. Uhler and Lugger (1876) noted the pinfish in the Sinepuxent drainage area of Chincoteague Bay (which bay this was is uncertain, perhaps near Station 4). Fowler (1913) captured one specimen at Ch.

Ephippidae — Spadefish Family

41. *Chaetodipterus faber* (Broussonet). Atlantic spadefish.

A single fish (140 mm) was collected by beach seining in Watt's Bay in July, 1947, by Mr. M. Castagne of the Franklin City Laboratory. This species is a southern straggler that occasionally enters Chincoteague Bay.

Chaetodontidae — Butterflyfish Family

42. *Chaetodon ocellatus* Bloch. Spotfin butterflyfish.

Three specimens of this southern species were captured in Chincoteague Bay. One, 69 mm, was caught in a trap net three miles south of Station 4 by Arve (1960) on October 4, 1959. A 70 mm specimen was taken at Station 9 near FC by Mr. N. Jester, November, 1959, while a commercial crab fisherman captured an 80 mm specimen, November 12, 1959, near Piney Shoals in Chincoteague Bay.

Pomacentridae — Demoiselles

43. *Abudefduf saxatilis* (Linnaeus). Sergeant major.

The sergeant major is known from six specimens, 80-110 mm standard length, taken in Watt's Bay and near FC September 24, 1958.

Labridae — Wrasse Family

44. *Tautoga onitis* (Linnaeus). Tautog.

The tautog is very common at the Ocean City and Chincoteague inlets and at Station 1; occasionally south to Station 4. Especial preference is shown by this species for the rocky areas around the Ocean City inlet and in Isle of Wight Bay north of Ocean City, Maryland. Within Chincoteague Bay proper, a specimen 70 mm standard length was captured January 20, 1958. Several others were captured near Newport Bay (Station 4) in wire traps (Arve, 1960).

This species is usually taken by hook and line. None were captured by beach seine or crab pot. Fowler (1913) examined specimens from Ch.

45. *Tautoglabrus adspersus* (Walbaum). Cunner.

A 115 mm specimen was captured in a crab pot at Parnell Bay in Chincoteague Bay November, 1959. Undoubtedly, others occur, grazing near rocks or pilings where the trawl or crab pots were not operated.

Trichiuridae — Cutlass Fish Family

46. *Trichiurus lepturus* Linnaeus. Cutlass fish.

A single 500 mm specimen was caught by Mr. N. Jester in July, 1956, in Watt's Bay near Ch. This is a southern species which frequents the area as well as Chesapeake Bay during periods of high water temperatures and high salinities. Lugger (1877), Goode and Bean (1879), Fowler (1933) reported this species either at OC or at Ch.

Gobiidae — Goby Family

47. *Gobiosoma bosci* (Lacépède). Naked goby.

A common goby throughout the oyster bed area (Wells, 1958) of both bays which ranges roughly the length of the bays along the western shore. This diminutive species eluded trawl or traps, but was taken, usually in shallow water, in special oyster trays (5x18x41 inches) set over the length of the bay and during the entire year. This goby lives most of its life in or near empty oyster shell "boxes." Examination of these "boxes" usually produced individuals varying from 15 to 58 mm in length. Gobies are least active during the winter months from December to March, weathering out the cold waters usually one per shell. This species breeds during May to middle July. Contrary to Gunter (1945) this species was taken in salinities greater than 20 parts per thousand. Uhler and Lugger (1876) noted this species only in Sinepuxent Bay; however, they most likely overlooked it because of its shy and secretive nature. Fowler (1913B) found specimens of this species in the stomach contents of a merganser (*Mergus americanus*) at Ch.

48. *Gobiosoma ginsburgi* Hildebrand and Schroeder. Seaboard goby.

Two seaboard gobies, 48 and 51 mm, were taken in August and September at Station 9. *G. ginsburgi* prefers higher salinities than does *bosci* and thus will be found more often in that area of Chincoteague Bay from Franklin City southward or around the Ocean City inlet. Of the hundreds of gobies seen and captured by the oyster tray method (see comments under *G. bosci*), only two *ginsburgi* were found. These specimens were taken in 12 feet of water over a sand bottom and near oyster plantings which like *bosci*, it must also inhabit or utilize.

Triglidae — Searobin Family

49. *Prionotus carolinus* (Linnaeus). Northern searobin.

This species is present from May to September from Station 8 south. Most specimens, varying in length from 175-190 mm, were usually taken in the deep channel of the Chincoteague inlet. An occasional specimen is caught with hook and line on the Ocean City, Maryland inlet jetty. Fowler (1913) records this species from Ch.

Blenniidae — Blenny Family

50. *Chasmodes bosquianus* (Lacépède). Striped blenny.

The striped blenny is found associated with oyster shells throughout the two bays. Specimens 12-109 mm are common. Specimens larger than 25 mm can usually be obtained all year by a search of oyster "boxes." This species lays ovoid eggs attached to oyster shells in May and June. I have seen one 45 mm specimen caught on hook and line at the Ocean City inlet. Usually this method of capture is uncommon because of the striped blenny's size.

51. *Hypsoblennius hentzi* (LeSueur). Feather blenny.

Little is known of this rare Maryland blenny. Specimens (80 mm) were taken from Hardy's Hole (near George Island Landing) November 14, 1957, and Tom's Cove (southeast of Chincoteague, Virginia) September 14, 1959 (92 mm), and in oyster trays from the Maryland-Virginia state line southward. This blenny is apparently similar in habitat preference and habits to *G. bosci*, *G. ginsburgi* and *Chasmodes bosquianus*. *Hypsoblennius* associates with oysters in the more saline portion of Chincoteague Bay south of White Rock (Station 7) more often than does *Chasmodes*.

Stromateidae — Butterfish Family

52. *Poronotus tricanthus* (Peck). Butterfish.

Noted only in May and August by this survey, although the butterfish must occur commonly in the bays from May to October. Commercial gill net operations took 20 pounds at Foxhill Levels (Station 6) in September, 1959. Perhaps individuals or small schools from the offshore populations enter the bay for short periods. Uhler and Lugger (1876) found butterfish in Sinepuxent Bay while Fowler (1913, 1927, 1930) noted their common presence at Ch. Arve (1960) cites the trap net capture of butterfish north of Station 5.

Mugilidae — Mullet Family

53. *Mugil cephalus* Linnaeus. Striped mullet.

Striped mullets (300-360 mm) were captured near FC and in commercial gill net operations (150 pounds in 1959) near Station 2 (Beacon 17 and vicinity). Murphy (1960) tabulates 366 pounds of mullet caught in 1958 with catches greater than 1000 pounds being made in the bays (?) between 1929-39. Where the latter were made is not known. Fowler (1913_B) found seven and one-half inch specimens of this species in the stomach of a merganser at Chincoteague, Virginia.

Atherinidae — Silversides Family

54. *Menidia menidia menidia* (Linnaeus). Atlantic silverside.

This abundant species, varying from 87 to 132 mm frequents Sinepuxent and Chincoteague Bays between October and June. The silverside apparently moves into other areas as it is absent in the bays during June to October, only one 50 mm specimen was taken in July. Fowler (1913) notes this species near Ch and OC (1945), while in 1913 and 1918 he found *M. beryllina* at (?) Assateague Island and in Sinepuxent Bay. The latter was not encountered during this survey nor has it been taken in beach samples in 1957 or 1958. *Menidia* sp. have been found in a merganser stomach at Ch. (Fowler, 1913_R).

Bothidae — Left Eye Flounder Family

55. *Paralichthys dentatus* (Linnaeus). Summer flounder.

The summer flounder, locally known as "fluke," is present over sandy bottoms from April through December with greatest concentrations adjacent to either inlet, May to July. A huge sport fishery exists at Stations 1, 2, 11 and 12 for this species. Specimens usually vary from 250 to 290 mm standard length with only an occasional large specimen taken at either inlet of up to 667 mm standard length. Flounders did not occupy the central portion of Chincoteague Bay until July when they were found throughout both bays. Trawling hampered by the dense beds of algae and bryozoans proved a poor method of sampling for this species. Traps or crab pots were more efficient means of capture as up to 16 could be caught in a Chincoteague Bay crab pot. Summer flounders utilize both inlets and begin to move out of the bays by August. The central portion of Chincoteague Bay is devoid of summer flounder by November. A residual population, however, can be found between Stations 1-5, apparently utilizing the last warm water areas of Chincoteague and Sinepuxent Bays (Table II). One summer flounder tagged at Station 4, August 28, 1959, was captured 312 days later, July 5, 1960, one mile south of the Ocean City Inlet for a net migration north of 10 miles.

56. *Scophthalmus aquosus* (Mitchill). Windowpane.

Small individuals, 80-90 mm, are found September to May in the inlets as well as from Station 1 south to Station 4 in Sinepuxent Bay. Adults over 230 mm are usually found over sandy bottoms near either inlet (Stations 1 and 12) from September to March. This species was captured by Fowler (1913) at FC and Ch.

Pleuronectidae — Righteye Flounder Family

57. *Pseudopleuronectes americanus* (Walbaum). Winter flounder.

Locally the winter flounder, called "black-back" or "halibut" is present throughout both bays from December to May especially in the deeper waters. Specimens, 243-318 mm standard length, are usually fat in December. Tagging failed to indicate any preference of pattern or movement. The inlet used most frequently as an avenue

of entry and dispersal is not known. Fowler (1913) found winter flounder at Ch.

Soleidae — Sole Family

58. *Trinectes maculatus maculatus* (Bloch and Schneider). Hogchoker.

This sole is present throughout the bays from August to October. Individuals commonly encountered measured 108-232 mm standard length. The hogchoker was expected in greater abundance, but was found only occasionally. No pattern of movement or area preference was evident.

Echeneidae — Remora Family

59. *Echeneis naucrates* Linnaeus. Sharksucker.

Numerous specimens 12-16 inches long were captured in May-September, 1958 and 1959 in commercial crab pots in Chincoteague Bay from approximately the Maryland-Virginia state line southward. Sharksuckers have been observed entering the bay attached to *Rhinoptera*, *Dasyatis*, *Mustelus* or *Squalus*.

Gobiesocidae — Clingfish Family

60. *Gobiosox strumosus* Peters. Skilletfish.

This diminutive species (12-67 mm) is present throughout both bays all year in association with oysters and *G. bosci*, *G. ginsburgi* and *C. bosquianus*. It spawns from late May through July. Normally it is found clinging to oysters or pilings in shallow water seldom over six feet deep. It spends its entire life in association with oysters.

Balistidae — Triggerfish and Filefish Family

61. *Alutera schoepfi* (Walbaum). Orange filefish.

Two individuals (210 mm) were taken at FC in July, 1959. Commercial crab fishermen south of Station 7 often catch this species. Fowler (1930) noted the orange filefish in the pound nets near Wallops Island just south of Chincoteague inlet.

62. *Balistes vetula* Linnaeus. Queen triggerfish.

Numerous specimens (160-250 mm) of this southern species were captured in commercial crab pots from approximately the Maryland-Virginia state line southward. One 160 mm specimen was captured on hook and line at FC.

Tetraodontidae — Puffer Family

63. *Sphaeroides maculatus* (Bloch and Schneider). Northern puffer.

The puffer, varying from 127 to 292 mm, is common May to October in the southern portion of Chincoteague Bay south of White Rock (Station 7), occasionally to Newport Bay (near Station 4) (Arve, 1960). It was extremely abundant at Stations 9 and 10 near FC. This species was found only at the deeper stations of Chincoteague and Sinepuxent Bays (Stations 2, 3, 4, 9 and 11) from August to October. Fowler (1913) found it at FC and Ch.

Diodontidae — Porcupine Fish Family

64. *Chilomycterus schoepfi* (Walbaur). Striped burrfish.

Three burrfish (105-127 mm) were captured September 2, 1959, at Stations 8 and 10. No young of this species were taken in the study area. Adults were captured in crab pots near Newport Bay (Station 4) in 1956. This species is apparently present throughout the lower Chincoteague Bay during the latter part of the summer and perhaps early fall.

Batrachoididae — Toadfish Family

65. *Opsanus tau* (Linnaeus). Oyster toadfish.

Collected from July to September; however, toadfish most likely frequent the bays all year. Individuals (98-223 mm) were taken at Stations 3, 5, 7, 9 and 10. Fowler (1927, 1930) found toadfish at Ch and Co.

DISCUSSION

Sixty-five species of 40 families and 59 genera were recorded within the limits of Chincoteague and Sinepuxent Bays during the present study. Specimens were captured mainly during trawling operations, but other data from 1957-59 beach seinings, oyster trays and interested people have been incorporated.

Since 1876 a total of 99 species (Table III) have been recorded within some portion of Sinepuxent or Chincoteague Bays, primarily adjacent to each inlet or where the present northern inlet exists. Of the 65 species noted to currently occupy the area, 23 have not been previously reported.

TABLE III.—Species known to inhabit Sinepuxent and Chincoteague bays or their inlets

Species	A U T H O R I T Y						
	Uhler & Lugger	Lugger	Goode & Bean	Fowler	Murphy	Arve	Schwartz
<i>Carcharias taurus</i>	x	x
<i>Mustelus canis</i>	x	x
<i>Carcharinus milberti</i>	x	(x)
<i>Squalus acanthias</i>	x
<i>Raja eglanteria</i>	x	x
<i>Raja ocellata</i>	x
<i>Dasyatis americana</i>	x	x
<i>Dasyatis sayi</i>	x
<i>Gymnura micrura</i>	x
<i>Rhinoptera bonasus</i>	x	(x)
<i>Acipenser (sturio) oxyrinchus</i>	x
<i>Megalops atlantica</i>	x
<i>Alosa mediocris</i>	x

TABLE III. (continued)

<i>Alosa pseudoharengus</i>	x	x
<i>Alosa sapidissima</i>	x	x
<i>Brevoortia tyrannus</i>	x	..	x	x
<i>Clupea harengus</i>	..	x	x
<i>Anchoa h. hepsetus</i>	x
<i>Anchoa m. mitchilli</i>	x	x
<i>Osmerus mordax</i>	..	x
<i>Esox niger</i>	x ?
<i>Synodus foetens</i>	x
<i>Bagre marinus</i>	x
<i>Ictalurus catus</i>	x ?
<i>Anquilla rostrata</i>	x	..	x	x
<i>Strongylura marina</i>	x	x
<i>Cyprinodon variegatus</i>	x	x
<i>Fundulus heteroclitus</i>							
<i>macrolepidotus</i>	x	x
<i>Fundulus luciae</i>	x	x
<i>Fundulus majalis</i>	x	x
<i>Lucania parva</i>	x	x
<i>Gambusia affinis</i>	x
<i>Gadus morhua</i>	x
<i>Merluccius bilinearis</i>	x
<i>Urophycis regius</i>	x
<i>Apeltes quadracus</i>	x
<i>Gasterosteus aculeatus</i>	..	x	..	x
<i>Fistularia tabacaria</i>	..	x
<i>Hippocampus erectus</i>	x	x
<i>Syngnathus floridae</i>	x
<i>Syngnathus fuscus</i>	x	x
<i>Centropristes striatus</i>	x	..	x	x
<i>Roccus americanus</i>	x	..	x	..
<i>Roccus saxatilis</i>	x	x
<i>Perca flavescens</i>	x
<i>Pomatomus saltatrix</i>	x	..	x	x
<i>Rachycentron canadum</i>	x
<i>Alectis crinitis</i>	..	x
<i>Caranx crysos</i>	..	x	x	x
<i>Selene vomer</i>	x	x
<i>Seriola (lalandi) dumerili</i>	x
<i>Vomer setipinnis</i>	x
<i>Orthopristis chrysopterus</i>	x	x
<i>Bairdiella chrysura</i>	x	x
<i>Cynoscion nebulosus</i>	x
<i>Cynoscion regalis</i>	x	x
<i>Larimus fasciatus</i>	x
<i>Leiostomus xanthurus</i>	x	x	x
<i>Menticirrhus americanus</i>	x
<i>Menticirrhus saxatilis</i>	x	x
<i>Micropogon undulatus</i>	x	x	x
<i>Pogonias cromis</i>	x
<i>Sciaenops ocellata</i>	x
<i>Archosargus probatocephalus</i>	x

TABLE III.—(continued)

<i>Lagodon rhomboides</i>	X	X	..	X	(X)
<i>Stenotomus chrysops</i>	X
<i>Chaetodipterus faber</i>	X
<i>Chaetodon ocellatus</i>	X	X
<i>Abudefduf saxatilis</i>	X
<i>Tautoga onitis</i>	X	..	X	X
<i>Tautogolabrus adspersus</i>	X
<i>Trichiurus lepturus</i>	..	X	X	X	X
<i>Sarda sarda</i>	X
<i>Scomberomorus maculatus</i>	X
<i>Gobiosoma bosci</i>	X	X
<i>Gobiosoma ginsburgi</i>	X
<i>Prionotus carolinus</i>	X	X
<i>Prionotus (strigatus) evolans</i>	X
<i>Astroscoptes guttatus</i>	X
<i>Chasmodes bosquianus</i>	X
<i>Hypsoblennius hentzi</i>	X
<i>Peprilus alepidotus</i>	X	X
<i>Poronotus triacanthus</i>	X	X	..	X	X
<i>Mugil cephalus</i>	X
<i>Mugil curema</i>	X
<i>Menidia b. beryllina</i>	X
<i>Menidia m. menidia</i>	X	X
<i>Etropus microstomus</i>	X
<i>Paralichthys dentatus</i>	X	..	X	X
<i>Scophthalmus aquosus</i>	X	X
<i>Pseudopleuronectes americanus</i>	X	X
<i>Trinectes m. maculatus</i>	X	X
<i>Gobiesox strumosus</i>	X
<i>Echeneis naucrates</i>	X
<i>Alutera schoepfi</i>	X
<i>Balistes vetula</i>	X
<i>Sphaeroides maculatus</i>	X	..	X	X
<i>Chilomycterus schoepfi</i>	X
<i>Opsanus tau</i>	X	..	X	X

(X) Tentatively included from sight record or captured in previous years but not during the period of study.

Species known from offshore waters along Assateague Island from Ocean City, Maryland, to Chincoteague, Virginia, but which have not currently been taken or known to enter these bays are: *Scomberomorus maculatus* (which supports a huge winter, December-February, drift gill net fishery 2-5 miles off Chincoteague, Virginia); *Stenotomus chrysops*; *Menticirrhus americanus* (April-May); *Raja erinacea* and *Raja ocellata* (comprising 50-70% of the industrial scrap fish industry off Ocean City, Maryland); *Cynoscion nebulosus* (present September-November); *Prionotus evolans* (another component of the June-August scrap fish industry); and *Rachycentron canadum*. Tarpon, *Megalops atlantica*, although noted by Fowler (1930) in the pound nets near Chincoteague, Virginia, have not authentically been taken from the bays. Specimens of tarpon up to 88 pounds in weight

have been caught recently with hook and line in Virginia seaside bays to the south of Chincoteague, Virginia.

The permanent opening of the northern inlet at Ocean City, Maryland in 1933 has produced a profound change in the fish fauna of Sinepuxent Bay which once had much lower salinities than those of today. Commercial records 1890-1958 compiled by Murphy (1960) indicate notable shifts in the populations which once inhabited Sinepuxent Bay and undoubtedly Chincoteague Bay of such species as: shad, *Alosa sapidissima* (commercial catch was 51,800 pounds); alewives, *Alosa pseudoharengus* (592,000 pounds); pike (most likely *Esox niger*, 54,025 pounds), yellow perch, *Perca flavescens* (72,000 pounds); white perch, *Roccus americanus* (77,680 pounds); and catfish (probably *Ictalurus catus*, 20,000 pounds). Pearson (1931) mentioned the effect of the periodic closing on such species as: *Micropogon undulatus*, *Cynoscion regalis*, *Leiostomus xanthurus* and *Pomatomus saltatrix*.

Seasonal water temperatures and, to a smaller degree, salinities are important factors influencing and limiting the distribution of species within the study areas. In general, these shallow bodies of water act as excellent nursery grounds for young of the spot (*Leiostomus xanthurus*), weakfish, (*Cynoscion regalis*), silver perch (*Bairdiella chrysura*), summer flounder (*Paralichthys dentatus*), anchovies (*Anchoa mitchilli*), black sea bass (*Centropristes striatus*) as well as a host of smaller sized species such as gobies, blennies, etc.

A constant oscillation of populations was found to exist in the two bays studied. Winter flounders and hogchokers moved in to occupy the area during winter months along with such forage species as silversides and anchovies. Gradually, spotted hakes and summer flounders moved into the area with a disappearance of winter flounders and silversides during the summer months that followed. Black sea bass populations overlapped each of the above shifts during the period April to November. Spot, by June, moved into the bays, in mass, to be later replaced, at least in the lower portion of Chincoteague Bay, by the weakfish, porcupine fish, swellfish and lizardfish. Occasional southern stragglers, namely the butterfly fish (*Chaetodon ocellatus*) appeared during periods of high salinities and water temperatures. The inlets were characteristically populated by sharks, rays, skates, tautog, summer flounder, kingfish and bluefish.

The influence of the older, natural southern inlet on the distribution patterns of fish within the bays is most pronounced. The influence of the newer permanent northern inlet today is effective, at most, only as far south in Sinepuxent Bay as Beacons 11 and 12 (5-8 miles). The influence of the various inlets can be vividly shown hydrographically (Pritchard, 1960) through the distribution of fishes and by means of the patterns and distribution of other organisms. High salinities are influential in limiting the distributions of the cancerid and portunid crabs [*Cancer irroratus* (Sieling, 1957) and *Ovalipes ocellatus*] to the inlets or at most to Stations 1, 2, 11 and 12. *Cragon*

septemspinosa, a crustacean, is abundant throughout the bays during the period October to May and its greatest numbers were recorded in the southern portion of Chincoteague Bay or around the inlets or areas of high salinity. It is replaced during June to August by *Paleomonetes vulgaris*. The crustacean *Chloridella empusa* was also found in August near Stations 8 to 9 in the southern part of Chincoteague Bay. It probably utilized the Chincoteague inlet to enter this area. Another crustacean *Libinia emarginata* taken from July to September was found only at Stations 1, 8, 9, 10, 11 and 12 or near the inlets, especially the southern. *Callinectes sapidus*, present throughout the entire bay, did not show greater abundance near either inlet. The importance of the southern inlet as an avenue of blue crab entrance into Chincoteague and/or Sinepuxent Bay was shown by Cargo (1954, 1959). A general southern migration of adult females of this crab persisted with little or no usage of the Ocean City inlet. The squid (*Lolliguncula brevis*) also responds to the influence of the various inlets. In April-May specimens 60-70 mm long are found throughout both bays except for Stations 5-9, greatest concentrations being at each inlet. In the summer it is found throughout the bays but with diminishing numbers near the center or Stations 5-7. Largest specimens (230 mm total length) occurred at each inlet. In the winter *Lolliguncula* is again most prevalent between Stations 1-2 and 9-12. The jellyfish (*Aurelia aurita*) was also found only in the high saline, southern portion of Chincoteague Bay from Cedar Islands (Station 8) southward. Its presence in that bay could only have been possible by utilization of the southern inlet. The limpet [*Diodora alternata* (Sieling, 1956)] invaded Chincoteague Bay via the southern inlet. Only the rock crab, *Cancer irrorata*, is known to have entered Chincoteague Bay via the northern inlet (Sieling, 1957).

CONCLUSIONS

Sixty-five species of fishes within 40 families and 59 genera currently are known to occur in Sinepuxent and Chincoteague Bays, 23 of which have never been previously reported. A total of 99 species are now known to have occurred since 1876.

These bays serve as excellent nursery grounds for a number of commercial species of fishes as well as some of lesser importance.

Fish distributions, hydrographic conditions and invertebrates, mainly crabs, squid and *Aurelia*, illustrate the predominant use of the southern inlet as an avenue of entry into the bays.

The cutting and establishment of the newer northern inlet at Ocean City, Maryland, has had a profound influence on the hydrography of Sinepuxent Bay. This has resulted in extinction, entry or redistributions of species. Periodic closure before the inlet's permanency often had the reverse effect on species abundance and distribution.

Little use today is made of the northern inlet as an avenue of entry by fishes into Chincoteague Bay. The fishes and other species,

namely sharks, flounders, tautog, lady crab and blue crab, that do enter Sinepuxent Bay by way of the Ocean City inlet are not usually found beyond the 5-8 mile southward influx of water from that northern entrance.

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Observations on Feeding Habits and Behavior of Grizzly Bears

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ABSTRACT: While engaged in a spawning-ground survey of salmon on the Nakina River, British Columbia, an excellent opportunity was afforded to study the feeding habits and behavior of several grizzly bears. The major food items and the manner in which they were obtained are discussed. Other behavior patterns such as territorialism and social hierarchy are likewise considered.

During the month of August 1959, observations were made by Alaska Department of Fish and Game biologists on the feeding habits and behavior of bears (*Ursus* sp.¹) on a 2-mile stretch of the Nakina River, a clear-water tributary of the Taku River. The Nakina is located in its entirety in British Columbia, while the Taku has its mouth about 30 miles south of Juneau, Alaska (Kerr, 1948). The Nakina is the major producer of an important stock of king salmon (*Oncorhynchus tshawytscha*), and the observations on bears were made in conjunction with a survey of salmon in this 2-mile stretch of water.

During the first two weeks of the study, abundant bear sign was evident, although only 1 or 2 bears were actually seen; these were sighted at a considerable distance from the camp. Then within 2 or 3 days, three bears took up residence in the vicinity of the camp and became quite imperturbable with respect to the survey party. These three were often encountered at extremely close range and fortunately paid little heed to the biologists. Besides these permanent "residents," 9 other bears were observed in the survey area, a few of these being seen fairly regularly while others were observed only once or twice. The individual bears were readily distinguished by obvious physical characters (size, color, etc.) as well as by behavioral peculiarities. The bears ranged in color from a light silvery-yellow through light and dark brown to a dark bluish-brown color. None of the bears was very large; an estimate of the weight of the largest was 600-700 pounds, with the more usual size about 500 pounds. All appeared to be in good condition.

FEEDING HABITS

Fish and berries were the major items of food eaten by bears during the study period, and in this respect feeding habits during the late summer were similar to those of the Kodiak Bear (Clark, 1957). King salmon and pink salmon (*Oncorhynchus gorbuscha*) were the major fish food; highbush cranberries (*Viburnum edule*)

¹ Information concerning the classification of the grizzly-brown bear group is inadequate to supply a specific name.

seemed to be the major plant material consumed. These findings were borne out by direct observation as well as by cursory examinations of droppings. When carcass surveys were made every other day (Table I), counted carcasses were slit lengthwise so that they would not be counted on subsequent days.

Only half-hearted attempts were made by the bears to capture live pre-spawned fish in good condition. In the few attempts in which we saw bears run and jump into a group of fish in a shallow riffle, they were never successful in catching one. For the most part they ate dead fish, although they would occasionally take a spawned-out fish which was still alive but not active enough to escape. In this respect, feeding habits of these grizzlies differed from those of bears along other river systems in Alaska, such as the Karluk River, where live fish are taken very frequently by brown bears (Shuman, 1950).

There did not seem to be any preference shown with respect to degree of decomposition of the dead fish eaten. A bear would travel along the river taking 1 or 2 bites from several fish and then suddenly take one into the brush and consume most or all of it. By the end of August the majority of the salmon had spawned and died, and most of the carcasses had floated downriver. Some of the dead fish, however, had lodged in the alders along the banks, among boulders, or in deep pools where the current was weak. These eventually became bloated and rose to the surface, where they were readily available to the bears. As a result, during the latter part of the survey period the bears utilized a greater percentage of carcasses which were in advanced stages of decomposition. Percentages were determined

TABLE I.—Percentage of king salmon carcasses fed upon by grizzly bears along a 2-mile stretch of the Nakina River, B.C., in 1959

Date	Total number of Carcasses counted	Percentage completely eaten ¹	Percentage partly eaten ²
Aug. 7	76	27.3	3.6
9	90	1.8	11.8
11	158	*	34.9
13	236	*	25.0
15	224	4.9	15.8
17	140	*	35.4
19	84	8.3	52.8
21	51	9.7	25.0
23	21	36.4	60.0

¹ Fish consumed to the point where they could not be sexed or measured.

² Fish with one or more bites that could be readily sexed and measured.

* Not recorded.

by recording, every other day during the month, the total number of carcasses available along the 2-mile stretch of water as well as the number of carcasses which had been eaten by bears.

King salmon carcasses were taken more frequently than pink salmon during the early part of the study period when the kings were much more abundant. Later in the month, the percentage of pinks utilized was slightly higher. Presumably this was because king carcasses were becoming less abundant towards the end of the month. When both species were available in large numbers, the bears seemed to prefer kings. In previous years, when red salmon (*Oncorhynchus nerka*) were more abundant, these fish were taken in proportionately greater numbers.

The percentage of carcasses eaten more or less in entirety, as well as the percentage which had one or two bites taken from them, increased gradually throughout the study period (Table I). Two obvious reasons for the increase are (1) that to maintain an equal intake of food material with decreasing numbers of fish, the bears would necessarily have to utilize a greater proportion of the total number of carcasses available as well as utilize a given carcass to a greater degree, and (2) that more individual bears were observed during the latter part of the survey.

BEHAVIOR

As previously mentioned, three bears comprised the "resident" group in the study area. At almost any time, at least one of them could be seen in the vicinity of the survey camp. Probably the main attraction here was a carcass weir built at the lower end of the 2-mile study area. This was a wire screen supported by tripods and extending across the entire width of the river. Carcasses of dead salmon floating downriver from above collected on this weir and were measured and sexed by the survey party twice a day. This accumulation of fish flesh was an ideal situation for the bears.

At times, bears other than the three residents would appear on the scene at the weir site. The strange bears were treated as intruders by the residents, and either the former or the residents would immediately panic and leave the scene; whether intruders or residents left depended upon the size of the intruding bears. The residents generally held their ground and forced strange bears to move out of the area; however, the sight of one non-resident bear, the largest seen in the area, would scatter the residents as soon as it made an appearance. The other animals seemed to be merely passing by and for the most part did not take advantage of the fish accumulated on the weir; at times strange bears even made wide detours of the weir to get from above to below it or vice versa. Whether this was due to intraspecific territorialism or to the presence of human scent at the weir site or to both is uncertain. An initial distrust of the weir was demonstrated by the resident bears, but this was rapidly dispelled and after a few days they even used it as a bridge to cross from one side of the river to the other or to the center section, where more carcasses

were collected. When the weir was removed after the survey was finished, one of the bears still came back to the site and appeared to be somewhat puzzled by its removal.

The three residents seemed to be quite tolerant of each other. Two were almost identical in appearance, being of the same size and color (silvery-yellow), and in fact were thought to be the same bear until they appeared together for the first time. From then on, their distinctive markings were quite obvious. The third member of the group was larger and darker in color than the other two, and was probably a year older. At least two of the three had been observed by Department biologists during similar spawning ground surveys in previous years. For the most part, a threatening attitude was taken by one of the bears only when one tried to maneuver a salmon carcass away from the other. Then they would face each other and growl or roar, sometimes keeping the noise up for several minutes, and make short, fierce charges. Once or twice during these encounters, the third bear would appear and make off with the fish while the other two continued their threat behavior. At times one of these three bears would come up unexpectedly and startle another one. Generally the startled bear would run off a short distance and then look around, see that the intruder was one of the other residents, and return to the activity which had been interrupted.

Two of the resident bears would often engage in play in the river, standing on their hind legs and cuffing each other, and then eventually go back to searching the pools and shores for dead fish. In one deep pool where carcasses collected in large numbers, they would swim around on the surface with the noses and eyes under water, apparently looking for carcasses. When a carcass was seen, it was brought to the surface with the hind feet, then transferred to the forepaws and eaten or discarded. Rarely one would submerge completely in retrieving a carcass.

There was no apparent social hierarchy displayed among the resident bears; no one bear in particular seemed to be dominant in the group.

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Observations on the Developmental Condition of Neonatal Birds¹

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ABSTRACT: The artificial incubation of eggs of about 100 species of wild birds was attempted. Egg and clutch weights, egg volumes, incubation periods, neonatal weights, interims between hatchings within clutches, number of days before hatching during which eggs float, and lengths of 6 of the long bones for neonates and adults are reported. Colors of natal down and of soft parts, especially of mouth linings, are given. Differences in extents of development at hatching are described, and some evolutionary postulates are discussed. This paper attempts to establish procedural standards under conditions that may allow for accurate and significant interspecific comparisons of incubation and neonatal condition independent of parental attentiveness and other environmental variables.

INTRODUCTION

The morphologic condition of development of hatching is used as an important criterion by ecologists and systematists in classifying birds (Daniel, 1957). An exhaustive search through North American museums in 1950 (Wetherbee, 1957), however, revealed that there were less than a dozen spirit specimens available that could confidently be called neonatal.

Terms like "precocial" and "altricial," "nidicolous" and "nidifugous," to indicate the extent of development at hatching have been generally used in ornithology, but critical examination reveals that the categories are oversimplifications and that there are actually a multitude of intermediate conditions. To re-examine this subject it was deemed necessary to have many specimens taken at the time of hatching.

Evans (1891, 1892) in Scotland and Heinroth (1908, 1922) in Germany hatched out many Old World species, but they did not carry on morphological work. Baldwin and Kendeigh (1932), Kendeigh (1940), and Graber (1955) investigated some parameters of artificial incubation of eggs of a few species of wild birds. Wetherbee (1958 and 1959) described the artificial incubation of more than 100 species of wild birds. In spite of the above-cited works, ornithologists generally have the erroneous belief that eggs of wild birds, especially of passerines, cannot be incubated artificially.

The lengths of 'natural' incubation periods of birds' eggs have been recorded throughout history. A great deal of those data are untrustworthy as Nice (1953; 1954) has indicated in her exhaustive review of the subject. Unfortunately, however, even the information

¹ Portions of these data were submitted to the University of Connecticut in partial fulfillment of the requirements for the Ph.D. degree.

² Contribution of the Dept. of Poultry Science and Massachusetts Cooperative Wildlife Research Unit supported by the University of Massachusetts, Massachusetts Division of Fisheries and Game, U.S. Fish and Wildlife Service and Wildlife Management Institute.

that is trustworthy (Kendeigh, 1952) is of little comparative value because of the environmental variables that presumably modify embryonic development and the incubation behavior of the sitting bird. Lack and Lack (1951) have shown, for example, that the period in *Apus apus* fluctuates between 18.5 to 24.5 days in the wild. Much greater margins of variability are encountered in the literature on incubation periods for individual eggs than I found in my experience with artificial incubation. A standardized method of incubation is needed.

Weights of wild birds' eggs have been most frequently taken under field conditions in which only crude determinations can be made.

Volumes of wild birds' eggs have been most often calculated from linear measurements (Amadon, 1943). As the shapes of birds' eggs vary widely, such indirect determinations are usually subject to wide error. A more direct method of determining volumes is needed.

Comparative descriptions of neonates, especially of the song bird species, have been practically nonexistent. Wetherbee (1957) summarizes those few data that have been published and indicates the need for specimens taken at the moment of hatching.

Quantitative data on extent of ossification at hatching are nonexistent for wild birds. Length of skeletal elements as a criterion of development is advocated by Hammet (1926): "... bone growth in length is largely due to increase in cell number while growth in weight is largely due to increase in cell size and density. The former is less affected by systemic determinants: sex, weaning, puberty." Hammet's work was based on rats. Dunn (1928) found "weight of the body . . . is a less reliable guide to the final size of the fowl (than the linear measurement) since it is highly variable (the coefficients of variation for bone length in the fowl are from about 3.5 to 4.5 per cent; body weight from about 12.18 per cent) . . ." Beebe *et al.* (1917) found that bone growth in birds becomes retarded a few hours before hatching and remains so until at least 24 hours after hatching.

Materials and methods for arriving at the data summarized in Table I are fully described in a previous paper (Wetherbee, 1959). In brief, incubation was at 37.8° C and 64 per cent relative humidity under forced draft conditions. Neonatal specimens were preserved in formaldehyde and prepared by potassium hydroxide corrosion, alizarin staining and glycerin clearing (see Williams, 1941). Measurements were made by vernier calipers.

COLOR OF MOUTH LININGS

Many species of birds have bright colorations inside the mouth and on expanded flanges of the rictal region. The hue varies with the species from yellow to red, and the rictal flanges also vary widely in size. Ticehurst (1910) stated that the conspicuous coloration serves as a target for the parent's regurgitative feeding and may even stimulate such behavior on the part of the parent. Cavity-nesting species

TABLE I.—Tabulated summary of notes on the artificial incubation and on the reproductive biology of various bird species

	Avg. egg wt.* (gms)	Avg. neonatal wt. (gms)	Avg. vol. (cc)	Avg. clutch wt. (gms)	Longest incu- bation (hrs)	Shortest hatch interim (hrs)
Green Heron <i>Butorides virescens</i>	16.08	13.05	80.39	72 ± 20
Black-crowned Night Heron <i>Nycticorax nycticorax</i>	35.95	107.9
Mallard <i>Anas platyrhynchos</i>	64.55
Wood Duck <i>Aix sponsa</i>	35.08	23.53	315.7
Black Vulture <i>Coragyps atratus</i>	98.27	75.70	196.5	16 ± 6
Broad-winged Hawk <i>Buteo platypterus</i>	40.60	29.63	39.17
Sparrow Hawk <i>Falco sparverius</i>	14.93	11.84
Ruffed Grouse <i>Bonasa umbellus</i>	16.03	13.24	534 ± 8
Bobwhite <i>Colinus virginianus</i>	10.23	7.52	559 ± 7
California Quail <i>Lophortyx californicus</i>	8.55	6.64	559 ± 7
Gambel's Quail <i>L. gambelii</i>	9.66	7.26	559 ± 7
Common Coturnix <i>Coturnix coturnix</i>	10.68	8.03	395 ± 15
Ring-necked Pheasant <i>Phasianus colchicus</i>	32.47	23.28	29.12	550 ± 0
Golden Pheasant <i>Chrysolophus pictus</i>	20.18	535 ± 0
Turkey <i>Meleagris gallopavo</i>	75.70
Guinea Chicken <i>Numida meleagris</i>	41.23	22.50	33.57	644 ± 6
Red Jungle Fowl <i>Gallus gallus gallus</i>	37.54	26.01	504 ± 0
Chicken (Sil.-Col. r. b.) <i>G. gallus domesticus</i>	48.41	37.15	48.41
Virginia Rail <i>Rallus limicola</i>	8.52	5.58
Killdeer <i>Charadrius vociferus</i>	12.74	9.89	50.95	0 ± 7
American Woodcock <i>Philohela minor</i>	15.55	13.10	46.63

TABLE I.—(continued)

	Avg. egg wt.* (gms)	Avg. neonatal wt. (gms)	Avg. vol. (cc)	Avg. clutch wt. (gms)	Longest incu- bation (hrs)	Shortest hatch interim (hrs)
Herring Gull <i>Larus argentatus</i>	60.60
Common Tern <i>Sterna hirundo</i>	18.86	12.09	19.29
Rock Dove <i>Columba livia</i>	16.87	12.22	414 ± 5
Mourning Dove <i>Zenaidura macroura</i>	7.52	5.15	15.03	27 ± 2
Domestic Parakeet <i>Melopsittacus undulatus</i>	2.39	1.67	405 ± 4
Ruby-th. Hummingbird <i>Archilochus colubris</i>	17 ± 17
Belted Kingfisher <i>Megasceryle alcyon</i>	9.33	33 ± 4
Yellow-shafted Flicker <i>Colaptes auratus</i>	7.21	4.80	7 ± 5
Downy Woodpecker <i>Dendrocopos pubescens</i>	2.08	1.67	8.32	5 ± 3
Eastern Kingbird <i>Tyrannus tyrannus</i>	3.97	2.43	3.27	10.10	366 ± 7	0 ± 5
Eastern Phoebe <i>Sayornis phoebe</i>	2.06	1.50	2.03	9.04	375 ± 0	11 ± 0
Horned Lark <i>Eremophila alpestris</i>	2.75	2.09	2.63
Tree Swallow <i>Iridoprocne bicolor</i>	1.80	1.34	1.72	346 ± 0
Bank Swallow <i>Riparia riparia</i>	1.47	1.04	1.41	7.79	36 ± 9
Rough-winged Swallow <i>Stelgidopteryx ruficollis</i>	1.84	1.29	1.77	367 ± 4
Barn Swallow <i>Hirundo rustica</i>	1.95	1.17	1.88	364 ± 0	48 ± 10
Cliff Swallow <i>Petrochelidon pyrrhonota</i>	2.14	1.62	2.07
Blue Jay <i>Cyanocitta cristata</i>	6.47	4.99	6.16	406 ± 0
Common Crow <i>Corvus brachyrhynchos</i>	18.61	16.15
Black-capped Chickadee <i>Parus atricapillus</i>	1.20	0.85	1.16	61 ± 10
Carolina Chickadee <i>P. carolinensis</i>	1.04	0.79	4.96	0 ± 10

TABLE I.—(continued)

	Avg. egg wt. * (gms)	Avg. neonatal wt. (gms)	Avg. vol. (cc)	Avg. clutch wt. (gms)	Longest incu- bation (hrs)	Shortest hatch interim (hrs)
White-breasted Nuthatch <i>Sitta carolinensis</i>	2.23	1.63	2.17	351±5
House Wren <i>Troglodytes aedon</i>	1.41	1.08	1.44	330±5
Bewick's Wren <i>Thryomanes bewickii</i>	1.36	1.11	9.78	350±10
Carolina Wren <i>Thryothorus ludovicianus</i>	2.73	2.09	13.64
Mockingbird <i>Mimus polyglottos</i>	4.60	3.50	298±9
Catbird <i>Dumetella carolinensis</i>	3.87	2.85	3.74	15.43	317±3	12±5
Brown Thrasher <i>Toxostoma rufum</i>	4.70
Robin <i>Turdus migratorius</i>	6.39	5.02	6.29	21.20	295±1	43±10
Wood Thrush <i>Holocichla mustelina</i>	5.26	3.46	5.17	14.90	335±3	16±6
Eastern Bluebird <i>Sialia sialis</i>	2.92	2.17	2.94	14.27	329±6
Blue-gray Gnatcatcher <i>Poliophtila caerulea</i>	1.02	0.75	5.05	320±6
Loggerhead Shrike <i>Lanius ludovicianus</i>	4.56	3.33
Starling <i>Sturnus vulgaris</i>	7.10	5.27	6.88	37.77	16±5
White-eyed Vireo <i>Vireo griseus</i>	1.75	1.35	350±7
Red-eyed Vireo <i>V. olivaceus</i>	2.36	1.76	2.25	35±9
Warbling Vireo <i>V. gilvus</i>	1.65	1.23	1.75
Yellow Warbler <i>Dendroica petechia</i>	1.57	1.14	1.54	7.85	267±2
Chestnut-sided Warbler <i>D. pensylvanica</i>	1.41	0.97	1.41	264±4
Prairie Warbler <i>D. discolor</i>	1.38	0.98	5.51
Ovenbird <i>Seiurus aurocapillus</i>	2.50	1.88	2.65	1.13	16±0
Yellowthroat <i>Geothlypis trichas</i>	1.86	1.24	1.82	256±12	22±19

TABLE I.—(continued)

	Avg. egg wt.* (gms)	Avg. neonatal wt. (gms)	Avg. vol. (cc)	Avg. clutch wt. (gms)	Longest incu- bation (hrs)	Shortest hatch interim (hrs)
House Sparrow <i>Passer domesticus</i>	2.78	2.02	2.63	14.33	282 ± 3	10 ± 3
Red-winged Blackbird <i>Agelaius phoeniceus</i>	3.98	2.75	3.85	14.76	263 ± 1	23 ± 9
Common Grackle <i>Quiscalus quiscula</i>	6.76	4.96	6.57	310 ± 0	21 ± 0
Brown-headed Cowbird <i>Molothrus ater</i>	3.03	2.22	2.75	297 ± 6
Scarlet Tanager <i>Piranga olivacea</i>	3.38	2.70	3.40
Cardinal <i>Richmondia cardinalis</i>	4.27	12.62	298 ± 9
Rose-breasted Grosbeak <i>Pheucticus ludovicianus</i>	3.94	3.10	4.07	16.92	294 ± 5
Purple Finch <i>Carpodacus purpureus</i>	2.00	1.92
Rufous-sided Towhee <i>Pipilo erythrophthalmus</i>	3.82	3.07
Chipping Sparrow <i>Spizella passerina</i>	1.54	1.09	1.50	274 ± 10	22 ± 16
Field Sparrow <i>S. pusilla</i>	1.67	1.23	1.66	6.51	24 ± 8
Swamp Sparrow <i>Melospiza georgiana</i>	2.06	1.46	8.25
Song Sparrow <i>M. melodia</i>	2.35

* Not necessarily fresh eggs.

have brighter coloration of the mouth and wider flanges as an adaptation to the poor visibility of the parent in the dark chamber.

The black-billed cuckoo, catbird, horned lark, and blue-gray gnatcatcher were the only North American birds examined having actual markings superimposed on the bright mouth linings. I have seen African weaver finches among the Old World species in the spirit collection of the American Museum of Natural History that have the markings elaborately developed, being metallic in luster.

The variation in mouth colors are probably attributable to at least three different factors: (1) a horny yellow covering sheathing the bones of the bill; (2) a transitory red or orange coloring of the epidermis by pigments from the yolk, probably carotinoids; and (3)

differences in extent of the blood vascular bed. In the first category are the yellow mouths of the flycatchers, swallows, thrushes, wrens, titmouses, and starlings. Red coloration, often noticeable also in the skin of the body, is extremely well-developed in the red-winged blackbird and rose-breasted grosbeak. As these species feed on plant-eating insects rich in red carotinoids (Nester, Derby, and DeWitt, 1948), and since xanthophyll (lutein) is selectively deposited in the egg yolk (Peterson, Hughes, and Payne, 1939), it would seem logical to assume that the food of the parents determines the color of the hatchlings' mouths in these species.

Skin color of these species fades out a few days after hatching. Palmer and Kempster (1919) maintain that in chickens xanthophyll is excreted through the skin of the bird and is oxidized; egg laying replaces that excretory process later on. Nestling blackbirds and grosbeaks continue to feed on phytophagous insects; perhaps they do not concentrate so much xanthophyll as their ovulating mother. Virgin and Klusmann (Kline, Schultze, and Hart, 1932) have reported that the avian organism is able to convert xanthophyll into a provitamin or more probably into a growth vitamin (differing from carotene). The utilization versus excretion problem would seem to hold promise of solution by using the red-winged blackbird as an experimental animal.

The third of the factors determining mouth color, capillary vascularization of the mouth, is conspicuous in the sparrows. This vascularity may be adaptive for oxygen exchange in the nestling's mouth. This interpretation of mouth color is favored by reference to Daniel's (1957) contention that the early respiratory activity of "altricial" birds is relatively inefficient because of incomplete fusion of the parabronchi of the lungs.

The observation of Saunders (1956) that the neonatal cedar waxwing has violet-blue lines in the mouth should be further investigated. It is suggested that fruits eaten by the young may account for this character, for it did not come to my attention in artificially incubated neonates.

One is impressed by the applicability of Ticehurst's theory (*loc. cit.*) on rectal flanges and cavity-nesting when the neonatal Starling is examined. On the other hand, the neonatal mockingbird, hatched in an open nest, also has extremely large rectal flanges. The presence of flanges is so unevenly distributed among passerine families and among species having entirely different nesting habits that the functional significance of these structures should be re-examined.

WEIGHT OF EGGS IN RELATION TO CONDITIONS AT HATCHING

As the weight of an egg diminishes with age and incubation and as (for all practical purposes) a "fresh" egg does not exist in nature, it is necessary to use some other indication of egg size for purposes of drawing comparisons between species. Fortunately, sometime during incubation of all eggs, the air cell becomes large enough (by

utilization of stored food by the embryo) to cause the egg to have a specific gravity of unity, *i.e.*, neither sinks nor floats in water, which permits the calculation of volume. A comparison of egg volumes and neonatal weights in Table III shows that the chicks of the majority of the species weigh about 75 per cent of the egg (at sp.g. 1.0) weight. Variations from that norm might be considered to be adaptive in different species; great caution needs be exercised, however, in attributing simple functions. A chick heavy in proportion to the egg from which it came may require for its immediate postnatal life a store of resorbed but unassimilated yolk. All species examined, whether "precocial" or "altricial," had large amounts of such neonatal yolk. A chick could be proportionately heavy because of an evolutionary shortening of incubation period relative to body development or because of an evolutionary slowing down of body development relative to incubation period or to differences in weights of yolk constituents and to differences in metabolic efficiencies. The ecologic requirements of a thinner shell or a smaller supply of water in a humid environment might also be contributing factors.

The brown-headed cowbird with its proportionately heavy chick (81%) may be adapted to its socially parasitic hatching by an evolutionary shortening of incubation period or a large store of yolk.

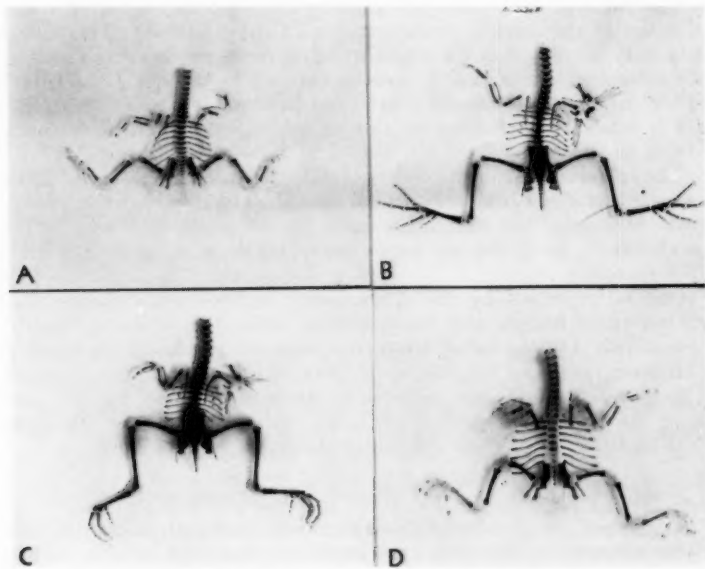


Fig. 1.—Comparison of ossification in neonatal birds. A. *Sialia sialis*, incubation period 13.5 days. B. *Coturnix coturnix*, 16.5 days. C. *Lophortyx californicus*, 23 days. D. *Cyanocitta cristata*, 17 days.

The blue jay (81% in Table III) has a slow body development relative to incubation period (compare Fig. 1 D with Fig. 1 A). The selective breeding that has brought about an increase in size of the chicken egg has only put more yolk in the neonate and has not lengthened the incubation period nor accelerated the body development. The incubation periods of both the domestic fowl and its supposed "ancestor," the red jungle fowl, are 21 days. Halbersleben and Mussehl (1921) found that chick (*Gallus*) weight was 64 per cent of egg weight regardless of differences in egg weight. At 35 days these weight differences had disappeared. My data for the eastern kingbird indicate that skeletal development was no more advanced in a neonate from an abnormally large egg than in neonates of that species hatched from normal-sized eggs.

The light relative weight (63%) of the common tern chick may be attributed to either the heavy shell or to lengthening of incubation period relative to rate of embryonic somatic development. Likewise the low value (67%) for wood thrush in Table III is correlated with a longer incubation period than that recorded for other turdids in Table I. The observed difficulty of yolk-sac resorption in this species may be related to that fact. The proportionate lightness of the four wood warblers, however, undoubtedly exemplifies an accelerated embryonic development that even their very short incubation period cannot counterbalance in restoring the 75 per cent norm. The bones of wood warblers are remarkably advanced in ossification at hatching.

INCUBATION PERIODS IN RELATION TO CONDITION AT HATCHING

The part that the length of incubation period plays in the condition of the young passerine bird at hatching has been mentioned above for the blue jay, which has a long (406-hour) period, and for the yellowthroat, which has a short (256-hour) period. Most other passerine species have periods between 280 and 370 hours (Table I), and their gross degree of ossification is much alike although certain bones vary from species to species. The yellowthroat, however, has a short (256-hour) period and a heavily ossified skeleton at hatching.

As the length of incubation period (Heinroth, 1908) is usually dismissed (erroneously) as the simple and proportional cause of differences in condition of young birds at hatching, it is perhaps appropriate to point to the common coturnix in Figure 1 B and to note that this exceedingly advanced neonate hatches in only 395 hours, 150 hours shorter than other species of quail which are less developed at hatching (Fig. 1 C).

Within the passerines the longer incubation periods produce the more helpless neonates, and the shorter periods produce the most advanced neonates. It can be summarized that a fast rate of embryonic development may shorten the incubation period but that a long incubation period does not produce a further advanced neonate.

INTERIMS BETWEEN HATCHING IN RELATION TO CONDITION
OF NEONATES

At least 13 species listed in Table I start to incubate before the last egg in the clutch is laid, as indicated by the known interval of at least a day between hatchings. These include:

Green heron	Black-capped chickadee
Domestic parakeet	Robin
Mourning dove	Red-eyed vireo
Belted kingfisher	Ovenbird
Yellow-shafted flicker	Common grackle
Bank swallow	Red-winged blackbird
Barn swallow	

The hypothesis could be made that benefits accrue to the first hatched in a brood of several competing nestlings. If this were so, we ought to expect that the species listed above would have a strong selective pressure exerted upon them for early hatching. An examination of the neonates of these species supports the hypothesis, for it is among the 13 species that the least developed neonates are encountered. The red-eyed vireo is an exception.

When there is an ecological requirement for a species to hasten its reproductive period, it is surmised that the hen, through natural selection, becomes broody before the last egg is laid, or even immediately after the first egg is laid. This selective pressure on the behavior of the female then results in a new set of selective pressures among the offspring to hatch early because they no longer hatch synchronously. The ecological requirement for hasty reproduction then acts upon the behavior of the adult and is secondarily facilitated and abetted by the young becoming available earlier for direct evolutionary physical response to the ecological requirement. I can conceive that this chain reaction could be an important mechanism through which the altricial condition in birds arose and is sustained. The "semi-precocial" hawks and herons may either be in the process of acquiring a more "altricial" condition or more likely are unable to achieve such a complete altricity as passerines without the benefit of evolutionary feed-back via paedomorphosis of the adult.

BONE SIZE AT HATCHING IN RELATION TO BONE SIZE OF ADULT

The extent of development at hatching expressed as a fraction of the completed ossification of the adult is influenced by at least three factors that may or may not be interdependent: (1) the rate of somatic development of the embryo; (2) the length of the incubation period; (3) the magnitude of total ontogenetic distance that adulthood represents for that species.

For purposes of this discussion, the growth patterns of the species indicated in Table III (derived in part from basic data of Table II) will be compared and possible significances emphasized. Different

TABLE II.—Average length of neonatal (a) and mature (k) bones in millimeters

Species	Stage	No.	Fe.	Tt.	Sc.	Co.	Hu.	UL
<i>Butorides</i>	a	2	10.3	12.6	6.8	3.8	7.6	8.1
<i>virescens</i>	k	2	48.8	80.5	42.8	36.5	67.3	75.0
<i>Nycticorax</i>	a	1	11.8	14.7	7.2	4.2	9.7	9.7
<i>nycticorax</i>	k	4	77.1	12.9	69.1	57.4	119.0	131.0
<i>Botaurus</i>	a	1	13.4	16.3	9.5	5.0	10.8	10.4
<i>lentiginosus</i>	k	3	78.7	129.0	63.4	56.3	108.0	122.0
<i>Aix sponsa</i>	a	2	13.6	24.6	10.2	6.0	9.6	7.8
	k	2	42.7	67.9	60.7	45.5	72.1	59.5
<i>Coragyps atratus</i>	a	1	21.0	27.9	12.4	5.5	14.5	15.0
	k	2	81.7	135.0	69.0	62.0	126.0	145.0
<i>Buteo lineatus</i>	a	1	11.4	13.7	7.2	3.4	10.4	10.4
	k	4	71.3	97.7	51.1	39.5	91.5	104.0
<i>B. platypterus</i>	a	1	12.8	14.9	7.5	3.8	11.0	11.0
	k	3	61.1	94.0	46.4	34.3	86.2	100.0
<i>Falco sparverius</i>	a	1	10.3	11.5	5.9	2.9	7.3	7.3
	k	3	36.2	48.8	28.4	24.2	44.8	47.6
<i>Bonasa umbellus</i>	a	1	14.7	20.4	10.5	5.7	9.0	8.5
	k	4	58.4	78.9	57.3	42.2	51.3	50.4
<i>Tympanuchus</i>	a	1	13.9	21.4	17.8	4.6	8.9	8.0
<i>cupido</i>	k	2	71.1	98.6	73.4	53.9	72.4	67.7
<i>Collinus</i>	a	2	11.8	17.0	8.6	4.5	6.0	5.4
<i>virginianus</i>	k	4	40.8	53.6	40.0	28.1	34.6	30.6
<i>Lophortyx</i>	a	1	11.8	17.3	8.7	4.7	6.3	5.1
<i>californicus</i>	k	3	40.7	55.9	40.9	28.4	33.2	28.8
<i>L. gambelii</i>	a	2	12.3	18.0	9.0	4.6	6.4	5.2
	k	2	40.7	56.0	41.5	27.9	33.4	29.9
<i>Coturnix coturnix</i>	a	1	11.4	15.4	9.0	4.8	6.4	5.3
	k	4	36.9	45.7	36.2	24.2	33.9	28.8
<i>Phasianus</i>	a	2	17.6	24.8	12.6	6.5	11.7	10.2
<i>colchicus</i>	k	4	80.6	109.0	74.2	53.2	73.5	66.9
<i>Gallus gallus</i>	a	2	17.5	23.6	12.8	7.2	10.6	10.0
	k	2	65.2	96.1	63.9	47.1	62.0	60.4
Chicken, Conn. (Sil.-Col. r. b.)	a	1	18.8	25.6	25.1	8.0	11.7	10.9
	k	4	101.0	146.0	93.0	69.0	90.0	88.0
<i>Rallus limicola</i>	a	1	11.4	16.9	7.8	3.0	6.9	5.5
	k	5	36.6	54.1	30.4	18.1	35.9	29.5
<i>Charadrius</i>	a	3	12.4	25.3	7.6	3.4	7.9	8.1
<i>vociferus</i>	k	3	26.5	52.1	29.0	18.5	39.1	44.1
<i>Philohela minor</i>	a	1	13.1	21.3	7.9	4.0	8.9	9.5
	k	5	37.7	54.7	37.8	25.8	43.9	48.6
<i>Larus argentatus</i>	a	1	17.0	35.0	13.2	5.0	15.8	15.9
	k	5	60.3	113.0	68.7	55.6	127.0	146.0
<i>Sterna hirundo</i>	a	2	10.8	17.2	8.6	3.6	9.0	9.8
	k	3	24.5	42.0	31.6	23.8	54.6	64.3

TABLE II.—(continued)

Species	Stage	No.	Fe.	Tt.	Sc.	Co.	Hu.	Ul.
<i>Columba livia</i>	a	2	8.2	9.4	4.4	3.2	5.2	6.4
	k	3	41.6	57.1	44.3	36.7	46.2	54.9
<i>Zenaidura</i>	a	2	6.6	7.6	4.2	2.8	4.4	5.1
<i>macroura</i>	k	4	28.8	38.6	33.7	25.8	32.6	38.0
<i>Melopsittacus</i>	a	2	4.2	4.8	2.2	1.6	2.5	2.2
<i>undulatus</i>	k	4	17.8	25.9	19.1	17.3	18.4	21.1
<i>Bubo</i>	a	1	13.7	16.1	7.8	4.2	12.9	12.8
<i>virginianus</i>	k	3	85.1	125.0	74.4	59.5	133.0	154.0
<i>Chordeiles minor</i>	a	1	8.2	11.3	5.8	3.2	5.8	6.8
	k	4	22.5	31.1	25.4	19.9	37.8	50.1
<i>Archilochus</i>	a	1	2.5	2.6	1.2	0.8	0.56	0.64
<i>colubris</i>	k	1	7.8	11.3	9.9	6.8	4.0	4.3
<i>Megasceryle</i>	a	2	9.8	11.4	5.2	3.6	7.0	8.0
<i>alcyon</i>	k	5	25.9	36.3	36.2	30.0	46.2	57.9
<i>Colaptes auratus</i>	a	2	4.8	5.6	1.7	1.2	2.9	3.0
	k	5	30.3	43.3	29.3	32.0	39.8	46.1
<i>Dendrocopus</i>	a	2	3.4	3.9	1.6	0.9	2.0	2.4
<i>pubescens</i>	k	5	16.4	25.4	14.8	18.1	22.2	26.6
<i>Tyrannus</i>	a	2	4.4	5.6	3.0	1.9	3.1	3.8
<i>tyrannus</i>	k	2	19.3	29.2	26.4	22.1	25.6	35.5
<i>Sayornis phoebe</i>	a	5	.35	4.6	2.9	1.7	2.6	3.2
	k	5	15.1	25.4	21.5	16.8	19.4	27.4
<i>Empidonax</i>	a	1	2.8	3.9	2.5	1.4	1.9	2.6
<i>minimus</i>	k	2	12.5	22.0	17.0	14.0	14.4	20.5
<i>Eremophila</i>	a	1	3.8	4.8	2.5	1.9	2.7	3.1
<i>alpestris</i>	k	2	20.1	33.4	25.3	20.9	24.9	29.4
<i>Iridoprocne</i>	a	5	2.7	3.7	1.9	1.5	1.6	2.3
<i>bicolor</i>	k	2	14.1	22.0	19.6	16.9	15.6	23.7
<i>Riparia riparia</i>	a	5	2.9	3.9	1.9	1.4	1.5	2.3
	k	3	12.4	19.7	16.3	14.5	12.9	19.8
<i>Stelgidopteryx</i>	a	4	3.2	4.3	2.2	1.7	1.9	2.7
<i>ruficollis</i>	k	1	13.0	20.8	18.3	16.0	15.9	24.8
<i>Hirundo rustica</i>	a	5	3.2	4.3	2.4	1.5	1.8	2.7
	k	2	13.1	21.0	19.3	15.6	15.5	23.7
<i>Petrochelidon</i>	a	4	3.5	4.4	2.3	1.6	1.8	2.4
<i>pyrrhonota</i>	k	2	14.0	23.0	20.0	17.3	16.0	24.5
<i>Cyanocitta</i>	a	5	5.4	6.8	3.7	2.3	3.6	4.1
<i>cristata</i>	k	5	32.1	52.4	30.7	26.5	32.7	38.0
<i>Corvus</i>	a	2	7.0	9.0	4.4	2.6	5.0	5.6
<i>brachyrhynchos</i>	k	5	51.5	87.9	50.6	44.3	66.8	81.0
<i>Parus atricapillus</i>	a	3	2.5	3.5	1.9	1.3	1.8	2.0
	k	4	12.9	23.8	13.9	13.3	14.2	18.1
<i>P. carolinensis</i>	a	3	2.6	3.9	1.9	1.2	1.8	2.0
	k	2	12.4	21.8	13.9	13.2	13.8	16.8
<i>Sitta carolinensis</i>	a	4	3.5	4.7	2.5	1.8	2.8	2.9
	k	5	15.9	25.5	17.5	16.4	19.1	24.3

TABLE II.—(continued)

Species	Stage	No.	Fe.	Tt.	Sc.	Co.	Hu.	Ul.
<i>Cinclus mexicanus</i>	a	1	3.6	5.1	2.8	1.9	2.6	2.9
	k	1	22.5	44.6	27.4	23.5	24.0	28.6
<i>Troglodytes aedon</i>	a	3	3.2	4.5	2.2	1.8	2.1	2.3
	k	4	14.5	23.1	14.1	13.1	13.6	14.2
<i>Thryomanes bewickii</i>	a	2	2.9	4.0	2.2	1.7	2.2	2.2
	k	3	13.7	23.5	13.6	13.0	14.1	15.7
<i>Thryothorus ludovicianus</i>	a	2	3.6	5.0	2.4	1.9	2.4	2.6
	k	4	17.3	29.1	16.7	16.2	16.7	17.7
<i>Mimus polyglottos</i>	a	3	4.9	6.4	3.3	2.2	3.2	3.7
	k	2	23.6	44.0	26.2	22.3	25.0	30.8
<i>Dumetella carolinensis</i>	a	5	4.2	5.9	3.1	2.0	2.9	3.3
	k	5	22.4	39.2	23.4	19.7	22.1	25.8
<i>Toxostoma rufum</i>	a	3	4.8	6.5	3.3	2.2	3.0	3.3
	k	5	27.9	48.1	28.2	24.1	27.4	30.1
<i>Turdus migratorius</i>	a	5	4.7	6.0	3.1	2.1	2.9	3.6
	k	5	27.3	46.0	31.3	26.6	28.8	35.4
<i>Hylocichla mustelina</i>	a	5	4.5	6.0	3.1	2.0	2.9	3.6
	k	5	23.6	41.6	25.6	22.8	23.9	29.1
<i>H. fuscescens</i>	a	1	4.0	5.5	3.0	1.8	2.7	3.2
	k	2	20.1	37.3	22.7	19.6	20.3	25.4
<i>Sialia sialis</i>	a	4	4.2	5.1	3.0	2.0	2.4	3.0
	k	3	17.6	30.0	32.3	19.2	20.4	27.5
<i>Poliophtila caerulea</i>	a	5	2.6	3.9	2.1	1.5	1.8	2.2
	k	2	10.8	20.9	11.6	10.6	12.0	14.9
<i>Bombycilla cedrorum</i>	a	2	3.7	4.7	3.0	2.0	2.3	2.8
	k	5	18.7	28.3	24.4	20.1	20.3	25.2
<i>Lanius ludovicianus</i>	a	1	5.0	7.1	3.3	2.3	3.3	3.3
	k	2	23.1	38.6	24.7	22.2	24.2	29.5
<i>Sturnus vulgaris</i>	a	4	5.1	6.7	3.5	2.3	3.0	3.5
	k	4	25.1	43.3	30.5	26.2	27.5	32.5
<i>Vireo atricapilla</i>	a	1	2.9	4.2	2.3	1.9	2.4	2.7
	k	1	12.6	23.0	14.6	11.7	12.4	14.3
<i>V. griseus</i>	a	2	2.8	4.2	2.4	1.7	2.2	2.5
	k	2	14.1	25.7	15.6	13.6	14.9	17.8
<i>V. bellii</i>	a	1	2.7	4.0	2.0	1.4	1.9	2.3
	k	2	13.0	24.4	13.5	12.6	13.1	15.5
<i>V. olivaceus</i>	a	2	3.7	5.0	3.0	2.0	2.4	2.9
	k	5	15.9	26.5	19.3	16.9	17.5	22.2
<i>V. philadelphicus</i>	a	1	4.1	5.9	3.4	2.4	2.8	3.3
	k	1	14.2	24.0	15.1	14.5	15.0	19.0
<i>V. gilvus</i>	a	2	3.6	4.8	2.6	1.7	2.3	2.6
	k	2	13.8	24.5	16.5	14.8	15.3	19.7
<i>Mniotilta varia</i>	a	1	3.3	4.6	2.7	1.9	2.2	2.5
	k	5	13.3	23.7	14.7	13.7	14.5	18.5
<i>Dendroica petechia</i>	a	2	2.8	4.2	2.0	1.5	1.9	2.3
	k	3	14.1	25.6	15.2	13.4	13.8	17.3

TABLE II.—(continued)

Species	Stage	No.	Fe.	Tt.	Sc.	Co.	Hu.	Ul.
<i>D. discolor</i>	a	2	2.8	4.4	2.2	1.6	2.0	2.3
	k	2	12.1	24.0	12.3	11.7	12.8	15.9
<i>Seiurus</i>	a	2	3.4	5.3	2.7	1.9	2.5	3.0
<i>aurocapillus</i>	k	5	16.8	30.1	19.5	16.9	18.2	22.0
<i>Geothlypis</i>	a	4	3.4	5.2	2.7	1.9	2.3	2.8
<i>trichas</i>	k	5	14.3	26.7	14.3	13.1	13.3	15.2
<i>Icteria virens</i>	a	1	3.2	5.1	2.9	1.9	2.5	2.9
	k	3	20.3	35.6	19.6	17.8	19.3	21.5
<i>Passer domesticus</i>	a	5	3.9	5.0	2.5	2.0	2.4	2.6
	k	5	18.2	29.1	22.1	18.8	18.7	20.9
<i>Agelaius</i>	a	4	4.0	5.6	2.8	2.0	2.9	3.2
<i>phoeniceus</i>	k	4	24.5	40.3	28.2	24.8	27.2	32.3
<i>Icterus galbula</i>	a	1	4.6	6.1	3.4	2.2	3.0	3.7
	k	5	20.7	34.9	23.1	20.5	21.8	27.0
<i>Quiscalus</i>	a	5	5.0	6.7	3.6	2.4	3.5	4.0
<i>quiscula</i>	k	5	31.8	51.4	35.2	30.5	33.1	38.2
<i>Molothrus ater</i>	a	5	4.1	5.7	3.0	2.0	2.8	3.2
	k	5	20.9	35.5	25.7	22.9	23.5	27.8
<i>Piranga olivacea</i>	a	1	3.9	5.4	3.0	2.1	2.9	3.2
	k	5	18.1	29.1	21.6	19.0	20.5	25.9
<i>Richmondia</i>	a	1	4.4	6.1	3.2	2.2	3.1	3.2
<i>cardinalis</i>	k	5	21.6	36.4	23.3	20.6	22.5	26.5
<i>Pheucticus</i>	a	3	4.5	5.9	3.4	2.0	2.9	3.6
<i>ludovicianus</i>	k	5	21.9	34.7	25.2	22.0	23.5	28.6
<i>Pipilo</i>	a	1	4.4	6.1	2.5	2.0	2.9	3.4
<i>erythrophthalmus</i>	k	4	23.3	38.7	23.3	20.2	22.5	23.9
<i>Spizella</i>	a	3	3.1	4.2	2.4	1.6	2.2	2.6
<i>passerina</i>	k	3	13.5	22.5	16.3	14.0	15.7	19.1
<i>S. pusilla</i>	a	3	3.4	4.9	2.3	1.7	2.2	2.6
	k	3	15.1	25.2	16.7	14.5	15.9	18.3
<i>Melospiza</i>	a	2	3.6	5.1	2.2	1.9	2.2	2.4
<i>georgiana</i>	k	3	17.6	30.0	16.4	14.5	16.1	16.1
<i>M. melodia</i>	a	1	3.3	4.8	2.4	1.7	2.3	2.4
	k	4	18.2	30.5	17.6	16.6	17.8	18.3

bones of any species have different degrees of linear maturation. Thus the femur of the killdeer is 47 per cent developed at hatching while its ulner is only 18 per cent developed. The ulna of the Virginia rail, another "precocial" bird, is 19 per cent developed, comparable with that of the killdeer, but its femur is only 31 per cent developed. Natural selection operates differentially on developmental rates of individual characters in addition to the developmental rates of the whole organism. It therefore would be more accurate to speak of a precocial character rather than of a precocious bird.

It is immediately obvious that the terms "precocial" and "altricial,"

TABLE III.—Average neonatal weight¹ and neonatal bone size²

Species	Avg. wt.	Avg. bone size						
		Fe.	Tt.	Sc.	Co.	Hu.	Ul.	Avg.
<i>Butorides virescens</i>		21	16	16	10	11	11	14
<i>Nycticorax nycticorax</i>		15	11	10	7	8	7	10
<i>Botaurus lentiginosus</i>		17	13	15	9	10	8	12
<i>Aix sponsa</i>		32	36	17	13	13	13	21
<i>Coragyps atratus</i>		26	21	18	9	12	10	16
<i>Buteo lineatus</i>		16	14	14	9	11	10	12
<i>B. platypterus</i>	.75	21	16	16	11	13	11	15
<i>Falco sparverius</i>		28	24	21	12	16	15	19
<i>Bonasa umbellus</i>		25	26	18	14	18	17	20
<i>Tympanuchus cupido</i>		20	22	24	8	12	12	16
<i>Colinus virginianus</i>		29	32	22	16	17	18	22
<i>Lophortyx californicus</i>		29	31	21	16	19	18	22
<i>L. gambelii</i>		30	32	22	16	19	17	23
<i>Coturnix coturnix</i>		31	34	25	20	19	18	25
<i>Phasianus colchicus</i>	.80	22	23	17	12	16	15	18
<i>Gallus gallus gallus</i>		27	24	20	15	17	16	20
<i>G. gallus domesticus</i>	.77	19	18	27	12	13	12	17
<i>Rallus limicola</i>		31	31	26	16	19	19	24
<i>Charadrius vociferus</i>		47	48	26	18	20	18	30
<i>Philohela minor</i>		35	39	21	16	20	20	25
<i>Larus argentatus</i>		28	31	19	9	12	11	18
<i>Sterna hirundo</i>	.63	44	41	27	15	16	15	26
<i>Columba livia</i>		20	16	10	8	11	12	13
<i>Zenaidura macroura</i>		23	20	12	11	13	13	18
<i>Melopsittacus undulatus</i>		24	18	12	9	14	10	15
<i>Bubo virginianus</i>		16	13	10	7	10	8	11
<i>Chordeiles minor</i>		36	36	23	16	15	14	23
<i>Archilochus colubris</i>		32	23	12	12	14	15	18
<i>Megasceryle alcyon</i>		38	31	14	12	15	14	21
<i>Colaptes auratus</i>		16	13	6	4	7	6	9
<i>Dendrocopus pubescens</i>		21	15	11	5	9	9	12
<i>Tyrannus tyrannus</i>	.74	22.7	19.1	11.3	8.5	12.1	10.7	14.1
<i>Sayornis phoebe</i>	.74	23.1	18.1	13.4	10.1	13.4	11.6	15.0
<i>Empidonax minimus</i>		22.4	17.7	14.7	10.0	13.1	12.6	15.1
<i>Eremophila alpestris</i>	.79	18.9	14.3	9.8	9.0	10.8	10.5	12.2
<i>Iridoprocne bicolor</i>	.78	19.1	16.8	9.6	8.8	10.2	9.7	12.4
<i>Riparia riparia</i>	.74	23.3	19.7	11.6	9.6	11.6	11.6	14.6
<i>Stelgidopteryx ruficollis</i>	.73	24.6	20.6	12.0	10.6	11.9	10.8	15.1
<i>Hirundo rustica</i>	.78	24.4	20.4	12.4	9.6	11.6	11.3	15.0
<i>Petrochelidon pyrrhonota</i>	.79	25.0	19.1	11.5	9.2	11.2	9.7	14.3

TABLE III.—(continued)

Species	Avg. wt.	Fe.	Tt.	Avg. bone size			UL.	Avg.
				Sc.	Co.	Hu.		
<i>Cyanocitta cristata</i>	.81	16.8	12.9	12.0	8.6	11.0	10.7	12.0
<i>Corvus brachyrhynchos</i>		13.5	10.2	8.6	5.8	7.4	6.9	8.7
<i>Parus atricapillus</i>	.73	19.3	14.7	13.6	9.7	12.6	11.0	13.5
<i>P. carolinensis</i>		20.9	17.8	13.6	9.0	13.0	11.9	14.4
<i>Sitta carolinensis</i>	.75	22.0	18.4	14.2	10.9	14.6	11.9	18.0
<i>Cinclus mex' anus</i>		16.0	11.4	10.2	8.0	10.8	10.1	11.1
<i>Troglodytes aedon</i>	.75	22.0	19.4	15.6	13.7	15.4	16.1	17.0
<i>Thryomanes bewickii</i>		21.1	17.0	16.1	13.0	15.6	14.0	16.1
<i>Thryothorus ludovicianus</i>		20.8	17.1	14.3	11.7	14.3	14.6	15.5
<i>Mimus polyglottos</i>	.76	20.7	14.5	12.5	9.8	12.8	12.0	13.7
<i>Dumetella carolinensis</i>		18.7	15.0	13.2	10.1	13.1	12.7	13.8
<i>Toxostoma rufum</i>		17.2	13.5	11.7	9.1	10.9	10.9	12.2
<i>Turdus migratorius</i>	.79	17.2	13.0	9.9	7.8	10.0	10.1	13.3
<i>Hylocichla mustelina</i>	.67	19.0	14.4	12.1	8.7	12.1	12.3	13.1
<i>H. fuscescens</i>		19.9	14.7	13.2	9.1	13.3	12.5	13.8
<i>Sialia sialis</i>	.74	23.8	17.0	9.2	10.4	11.7	10.9	13.8
<i>Polioptila caerulea</i>		24.0	18.6	18.1	14.1	15.0	14.7	17.4
<i>Bombycilla cedrorum</i>		19.7	16.6	12.2	9.9	11.3	11.1	13.5
<i>Lanius ludovicianus</i>		21.6	18.3	13.3	10.3	13.6	11.1	14.7
<i>Sturnus vulgaris</i>	.77	20.3	15.4	11.4	8.7	10.9	10.7	12.9
<i>Vireo atricapilla</i>		23.0	18.2	15.7	16.2	19.3	18.8	18.5
<i>V. griseus</i>		19.8	16.3	15.3	12.5	14.7	14.0	15.4
<i>V. bellii</i>		20.7	16.3	14.8	11.1	14.5	14.8	15.4
<i>V. olivaceus</i>	.78	23.2	18.8	15.5	11.8	13.7	13.0	19.0
<i>V. philadelphicus</i>		28.8	24.5	22.5	16.5	18.6	17.3	21.4
<i>V. gilvus</i>	.70	26.0	19.5	15.7	11.4	15.0	13.1	16.8
<i>Mniotilta varia</i>		24.8	19.4	18.3	13.8	15.1	13.5	17.5
<i>Dendroica petechia</i>	.73	19.8	16.4	13.1	11.1	13.7	13.2	14.6
<i>D. discolor</i>	.69	23.1	18.3	17.8	13.6	15.6	14.4	17.1
<i>Seiurus aurocapillus</i>	.75	20.2	17.6	13.8	11.2	13.7	13.6	15.0
<i>Geothlypis trichas</i>	.68	23.7	19.4	18.8	14.5	17.2	18.4	18.7
<i>Icteria virens</i>		15.7	14.3	14.7	10.6	12.9	13.4	13.6
<i>Passer domesticus</i>	.77	21.4	17.1	11.3	10.6	12.8	12.4	14.3
<i>Agelaius phoeniceus</i>	.71	16.3	13.8	9.9	8.0	10.6	9.9	11.4
<i>Icterus galbula</i>		22.2	17.4	14.7	10.7	13.7	13.7	15.4
<i>Quiscalus quiscula</i>	.75	15.7	13.0	10.2	7.8	10.5	10.4	11.3
<i>Molothrus ater</i>	.81	19.6	16.0	11.6	8.7	11.9	11.5	13.2
<i>Piranga olivacea</i>	.79	21.5	18.5	13.8	11.0	14.1	12.0	14.5
<i>Richmondia cardinalis</i>		20.3	16.7	13.7	10.6	13.7	12.0	14.5
<i>Pheucticus ludovicianus</i>	.76	20.5	17.0	13.4	9.0	12.3	12.5	14.1
<i>Pipilo erythrophthalmus</i>		18.8	15.7	10.7	9.9	12.8	14.2	13.7

TABLE III.—(continued)

Species	Avg. wt.	Fe.	Tt.	Avg. bone size			Ul.	Avg.
				Sc.	Co.	Hu.		
<i>Spizella passerina</i>	.73	22.9	18.6	14.7	11.4	14.0	13.6	15.0
<i>S. pusilla</i>	.74	22.5	19.4	13.7	11.7	13.8	14.2	15.0
<i>Melospiza georgiana</i>		20.4	17.0	13.4	13.1	13.6	14.9	15.4
<i>M. melodia</i>		18.1	15.7	13.6	10.2	12.9	13.1	13.9

¹ Expressed as ratio of hatchling weight/average egg volume.

² Expressed as per cent of adult bone length (Fe. = Femur; Tt. = Tibio-tarsus; Sc. = Scapula; Co. = Coracoid; Hu. = Humerus; Ul. = Ulnar; data derived from Table II).

used in ornithology to denote condition of development at hatching, are inapt in this kind of analysis. The altricial Philadelphia vireo and the precocial wood duck have the same neonatal bone size expressed as per cent of adult size. If the cartilages of the skeletal elements were included in these determinations, the altricial bird would have a great deal less distance to go than the precocial one in reaching adult size. It is patent, therefore, that in drawing comparisons between species of widely separated taxa the extent of development at hatching expressed in terms of per cent of adult development is undermined by some radical evolutionary phenomena.

The neonatal bones examined in most of the song birds average 13 to 15 per cent of their adult lengths. Exceptions to that figure are as follows (Table III):

The low (8.7%) value for the common crow is probably not simply a function of the large size of this species, for the blue jay, of the same family, also has a moderately low value (12.0%). An examination of the neonates and consideration of the length of incubation indicates that the low value is also a function of relatively slow rate of prenatal development. Among the other species having low values in this respect are the dipper, red-winged blackbird, and common grackle (11.0%). The latter two have strong sexual dimorphism in size, i.e., the male has an extended ontogenetic distance, which may account for a smaller size that is purely relative. The red-winged blackbird's delayed sexual maturity may be relevant in a consideration of slower developmental rate (proportionate to incubation period) of its embryos.

Three vireos have high values in Table III (21.4, 19.0, and 18.5%). As their neonatal bodies show heavy ossification, the values are probably a function of accelerated prenatal growth (but of moderately long incubation period). The answer to the puzzling question of why three of these vireos have natal down and three of them do not is apparently not tied to extent of bodily development (as expressed), for while the naked *Vireo griseus* and *V. bellii* have low values in Table III, the also naked *V. atricapilla* has a high value.

Another species having a high value is the yellowthroat (18.7%).

This species has a large egg for the size of the adult, a small neonate for the size of the egg, a short incubation period for its order, as well as a heavy ossification at hatching. The yellowthroat seems to be to the passerines what *Coturnix* is to the nonpasserines in respect to accelerated ontogeny.

There is no simple and direct correlation between adult body size of species and the neonatal bone size expressed as per cent of adult size.

RELATION OF EXTENT OF DEVELOPMENT AT HATCHING TO EXTENT AT MATURITY

Table IV presents two indices, which, when compared for each species, yield some measure of the degree of neonatal development for a certain character (ratio of humerus length to femur length). Column A shows that the humerus of the green heron has achieved at hatching only 52 per cent as much development as that of the femur. Column B shows that the adult humerus of the green heron is 138 per cent as large as the adult femur. Using this character throughout, a certain scale of relative precocity can be tentatively set up.

The American bittern is relatively further advanced than the green heron or the black-crowned night heron. The latter is less advanced than the green heron. One might postulate that ground nesting for the bittern may be conducive to greater precocity of the neonate.

Among the four Falconiformes examined, the black vulture is by far the more altricial. The other hawks show that the relative adult humeral lengths are proportionately reflected in the neonates. As hawks and herons are often called semi-altricial, it is of interest to note in Table IV that the herons are more precocial than the hawks.

In the Galliformes the domestic chicken is more precocious (for the character of shape under discussion) than is its ancestor, the red jungle fowl. The common coturnix, however, which by all other standards would seem to be highly precocious, is actually the least precocious of the lot.

An intriguing situation that should not be overlooked is that, where in evolution the adult may have come secondarily to resemble its specialized young (Wetherbee, 1958), precocity is determined more by evolutionary regression (of the adult) than by evolutionary progression (of the young). For example, no one can deny that the killdeer is extremely organized at hatching, but its organization when looked upon in terms of its adult characters is disconcerting; *i.e.*, the cursorial young killdeer is highly specialized for running. Its change in form during postnatal development is literally an ecologically based metamorphosis.

The gull and especially the tern are extremely altricial by the standards of Table IV; but this is more apparent than real, for actually the adults are highly specialized.

TABLE IV.—Reflection of adult characters (hu/fe) in extent of their development at hatching

Species	A ¹	B ²
<i>Butorides virescens</i>	.52	1.38
<i>Nycticorax nycticorax</i>	.53	1.54
<i>Botaurus lentiginosus</i>	.59	1.37
<i>Aix sponsa</i>	.41	1.68
<i>Coragyps atratus</i>	.46	1.54
<i>Buteo lineatus</i>	.69	1.46
<i>B. platypterus</i>	.62	1.41
<i>Falco sparverius</i>	.57	1.24
<i>Bonasa umbellus</i>	.72	.88
<i>Tympanachus cupido</i>	.60	1.02
<i>Colinus virginianus</i>	.59	.85
<i>Lophortyx californicus</i>	.66	.82
<i>L. gambelii</i>	.63	.82
<i>Coturnix coturnix</i>	.61	.92
<i>Phasianus colchicus</i>	.73	.91
Red Jungle Fowl	.63	.95
Domestic chicken (Columbian)	.89	.89
<i>Rallus limicola</i>	.61	.98
<i>Charadrius vociferus</i>	.40	1.48
<i>Philohela minor</i>	.57	1.16
<i>Larus argentatus</i>	.43	2.11
<i>Sterna hirundo</i>	.36	2.33
<i>Columba livia</i>	.55	1.11
<i>Zenaidura macroura</i>	.57	1.13
<i>Melopsittacus undulatus</i>	.58	1.03
<i>Bubo virginianus</i>	.62	1.56
<i>Chordeiles minor</i>	.42	1.68
<i>Archilochus colubris</i>	.44	.51
<i>Megasceryle alcyon</i>	.39	1.78
<i>Colaptes auratus</i>	.44	1.31
<i>Dendrocopos pubescens</i>	.43	1.35
<i>Tyrannus tyrannus</i>	.53	1.32
<i>Sayornis phoebe</i>	.58	1.28
<i>Empidonax minimus</i>	.58	1.15
<i>Eremophila alpestris</i>	.57	1.24
<i>Iridoprocne bicolor</i>	.53	1.11
<i>Riparia riparia</i>	.50	1.04
<i>Stelgidopteryx ruficollis</i>	.48	1.22
<i>Hirundo rustica</i>	.48	1.18
<i>Petrochelidon pyrrhonota</i>	.45	1.14

TABLE IV.—(continued)

Species	A ¹	B ²
<i>Cyanocitta cristata</i>	.65	1.02
<i>Corvus brachyrhynchos</i>	.55	1.30
<i>Parus atricapillus</i>	.65	1.10
<i>P. carolinensis</i>	.62	1.11
<i>Sitta carolinensis</i>	.66	1.20
<i>Cinclus mexicanus</i>	.68	1.07
<i>Troglodytes aedon</i>	.70	.94
<i>Thryomanes bewickii</i>	.74	1.03
<i>Thryothorus ludovicianus</i>	.69	.96
<i>Mimus polyglottos</i>	.61	1.06
<i>Dumetella carolinensis</i>	.70	.99
<i>Toxostoma rufum</i>	.63	.98
<i>Turdus migratorius</i>	.58	1.05
<i>Hylocichla mustelina</i>	.64	1.01
<i>H. fuscescens</i>	.67	1.01
<i>Sialia sialis</i>	.49	1.16
<i>Poliophtila caerulea</i>	.62	1.11
<i>Bombycilla cedrorum</i>	.57	1.08
<i>Lanius ludovicianus</i>	.63	1.05
<i>Sturnus vulgaris</i>	.53	1.10
<i>Vireo atricapilla</i>	.84	.98
<i>V. griseus</i>	.74	1.06
<i>V. bellii</i>	.70	1.01
<i>V. olivaceus</i>	.59	1.10
<i>V. philadelphicus</i>	.65	1.06
<i>V. gilvus</i>	.57	1.11
<i>Mniotilta varia</i>	.61	1.09
<i>Dendroica petechia</i>	.69	.98
<i>D. discolor</i>	.68	1.06
<i>Seiurus aurocapillus</i>	.68	1.08
<i>Geothlypis trichas</i>	.73	.93
<i>Icteria virens</i>	.82	.95
<i>Passer domesticus</i>	.59	1.03
<i>Agelaius phoeniceus</i>	.64	1.11
<i>Icterus galbula</i>	.62	1.05
<i>Quiscalus quiscula</i>	.67	1.04
<i>Molothrus ater</i>	.61	1.12
<i>Piranga olivacea</i>	.66	1.13
<i>Richmondia cardinalis</i>	.67	1.04
<i>Pheucticus ludovicianus</i>	.60	1.07
<i>Pipilo erythrophthalmus</i>	.68	.97

TABLE IV.—(continued)

Species	A ¹	B ²
<i>Spizella passerina</i>	.61	1.16
<i>S. pusilla</i>	.61	1.05
<i>Melospiza georgiana</i>	.67	.91
<i>M. melodia</i>	.71	.98

¹ Extent of potential development humerus has achieved at hatching (neo. hu./ad. hu.) expressed as ratio of extent of potential development femur has achieved at hatching (neo. fe/ad. fe), i.e., ratio of per cents.

² Length of adult humerus expressed as ratio of length of adult femur, i.e., ratio of sizes.

Among the swallows the bank and the tree swallow seem to be the more altricial in Table IV, although the fact of the matter is that the young of all swallows are practically identical. At this point in the analysis one is forced by weight of the accumulated evidence to resume the use of quotation marks around "altricial" and "precocial," for it is evident that the whole life history of the organism and its biogenetic burden are involved in any real understanding of the developmental condition of young at hatching. For further discussion see Wetherbee (1958).

CONCLUSIONS

The following general conclusions are drawn from the data:

1. Mouth markings in neonates, common in Old World species, were found in only four New World species: catbird, horned lark, blue-gray gnatcatcher, and black-billed cuckoo. Mouth color of neonates is perhaps partly the result of blood capillary beds, at least in the field sparrow. As parabronchi are poorly developed in "altricial" neonates, the mouth lining may serve as an accessory respiratory organ. Neonates of most bird species weigh 72 to 78 per cent of the weight of the egg (at specific gravity of unity) from which they hatch. As neonatal brown-headed cowbirds are heavy in proportion to the eggs from which they hatch, social parasitism may put selective pressure on length of incubation period and/or the amount of neonatal yolk. The neonatal blue jay, heavy in proportion to the egg from which it hatches, seems to have a slowing of body development relative to incubation period. The proportionately light neonate of the wood thrush on the other hand may be caused by an extended incubation period. The wood warblers, especially the yellowthroat, have unusual growth patterns comparable with that of the common coturnix: large egg for the size of the adult, small neonate for the size of the egg, short incubation period for its taxon, and advanced development at time of hatching.

2. Volume of egg does not affect the extent of development at

hatching within a species nor affect the length of incubation period at least appreciably within a species.

3. Most passerine birds have incubation periods between 280 and 370 hours. Examples of extremes are: blue jay, 406 hours, and yellowthroat, 256 hours. These incubation periods show very little variation under standardized conditions and are species specific.

4. The longer passerine incubation periods produce the more helpless neonates, and the shorter periods produce the most advanced neonates. Therefore, although a fast rate of embryonic development may shorten the incubation period, a long incubation period does not produce a further advanced neonate.

5. Commencement of incubation by the parent before the last egg of the clutch is laid probably exerts selective pressure for short incubation period because of intrabrood competition. The altricial condition in birds may have arisen through this mechanism. In conjunction with the genetic mechanisms of poicilogony (foetalization of adults) the selective mechanism above may provide a rather full understanding of the evolution of infants.

6. The qualities generally described by the terms "precocious" and "altricial" are less apt for species than for individual characters. Contrary to general understanding, some "altricial" birds have less ontogenetic distance to traverse in reaching maturity than some "precocious" birds.

7. Neonatal bone lengths (of the six bones examined) range from 4 per cent (coracid, yellow-shafted flicker) to 48 per cent (tibiotarsus, killdeer) of their adult lengths. The killdeer is the species with the highest average bone length (30% of adult size) at hatching ("the most precocious bird"). The crow is the "most altricial" (8.7% of adult size). Passerine species having the smallest neonatal bone sizes (expressed as per cent of adult sizes) in addition to the crow are dipper, red-winged blackbird and common grackle (11%). The black-capped, red-eyed and Philadelphia vireos, and the yellowthroat are the passerine species having the largest neonatal bone sizes, 18.5 to 21.4 per cent.

8. The extent of development at hatching is determined not only by the rates of character developments in the embryo and by the length of incubation period but also by the magnitude of total ontogenetic distance that adulthood represents for each character of each species; i.e., the whole life history of the organism and its biogenetic burden are involved in any real understanding of the developmental condition of young at hatching.

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The Genus *Skrjabinopsolus* (Trematoda: Digenea), with Reference to the Allocreadioid Problem¹

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ABSTRACT: In young adults of *Skrjabinopsolus manteri*, the excretory system has three flame cell groups per quadrant and other features like that of *Deropristis inflata*. The miracidium of *S. manteri* has one pair of flame cells and lacks an eyespot. Extensive morphological and ecological studies strongly suggest that the cercaria is the species previously reported for *Allocreadium ictaluri*; it encysts with little development in freshwater oligochaetes, on which the sturgeon feeds. In its embryology, the primary excretory pores develop in the tail of the cercaria a short distance from the body, thereby supporting the allocation of *Skrjabinopsolus* and related genera to a distinct family, the Deropristiidae. That family is redefined to include *Deropristis*, *Pristicola*, and *Skrjabinopsolus* in the Deropristiinae and *Cestrahelminis* as type and only genus in a new subfamily, Cestrahelmininae.

INTRODUCTION

The diversity of life histories and larval stages of trematodes that La Rue (1957) has assigned to the superfamily Allocreadioidea poses a major problem in the taxonomy of the Digenea. A group that is pertinent to that problem contains species of *Skrjabinopsolus* and related genera whose taxonomic position has been in dispute. One life history is known, that of *Deropristis inflata* reported by Cable and Hunninen (1942). The writer's observations indicate the probable life history of another species, *Skrjabinopsolus manteri*, which Cable (1952) described as a common parasite of the Shovelnose Sturgeon in the Wabash River. Its cercaria is believed to be the one described by Seitner (1951) as the larva of *Allocreadium ictaluri* but shown not to be such by the writer (Peters, 1957). As nothing is known concerning the embryology of the excretory system in the group, that aspect was investigated along with the life cycle of *S. manteri* for information bearing on the status of its group in the allocreadioid complex.

The genus *Skrjabinopsolus* was erected by Ivanov and Murygin (1937) to include *S. acipenseris* from sturgeons of the Volga River delta as type species and supposedly *Distomum semiarmatum* Molin, 1858, as a second species. Another, *S. skrjabini*, was reported from sturgeons of the Black Sea by Osmanov (1940) and differentiated from *S. acipenseris* in having a prepharynx and a greater posterior extent of the uterus. However, Bykhovskii and Dubinina (1954) examined specimens from sturgeons in both the North Caspian and Black seas and reduced *S. skrjabini* to synonymy with *S. acipenseris*.

¹ Based on part of a thesis submitted for the Ph.D. degree, Purdue University, August, 1960, and prepared under the direction of Professor R. M. Cable.

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Although their conclusion appears valid to the writer, Skriabin (1954) regarded the problem of speciation in the genus *Skrjabinopsolus* as still unsolved. It may be that *S. semiarmatum*, if better known, would prove to be the only valid European species of its genus. Molin (1858) reported it briefly from *Acipenser naccari* and extended his observations somewhat in a later report (1861). There is no known feature of the species which would exclude it from *Skrjabinopsolus*, and the heavy cuticular armature, sessile ventral sucker, and especially the spiny cirrus suggest its inclusion in that genus. Osmanov (translated from Markevich, 1951) supports that view, as follows:

"It is exceedingly possible that *Skrjabinopsolus skrjabini* n. sp. is identical with *Distomum semiarmatum* Molin, 1858, from *Acipenser sturio*. Consequently we regard our species as provisional for the present."

The only other species recorded for the genus is *S. manteri* which is very similar to *S. acipenseris* but differs from that species in having a much longer body with the ovary more anterior and eggs that average slightly smaller in size.

The occurrence of such similar trematodes only in sturgeons, and from such widely separated localities, is a striking example of host specificity among the digenetic trematodes and parallel evolution of host and parasite. Because a common gene pool cannot be shared by parasites of the strictly freshwater sturgeon in the Wabash River and those of Eurasian sturgeons, it is concluded that, although very similar, *S. acipenseris* and *S. manteri* are distinct species.

EVIDENCE CONCERNING THE LIFE CYCLE OF *SKRJABINOPSOLUS MANTERI*

The difficulties posed by Seitner's (1951) account for the life history of *Allocreadium ictaluri* were discussed by Cable (1956), who pointed out that the cercaria described by Seitner is much like that of *Deropristis inflata*, as indeed Seitner had observed. Because closely related trematodes often have extremely similar life cycles and the cercaria of *D. inflata* encysts in a marine annelid, fresh-water oligochaetes were collected from the Wabash River and examined for a metacercaria similar to that of *D. inflata*; such was quickly found and thereafter proved to result from the penetration and encystment of the cercaria described by Seitner. As in *D. inflata*, the metacercaria does not increase in size or develop appreciably except in spination, which becomes more conspicuous. The large excretory concretions remain intact.

The writer has confirmed Seitner's observations that the cercaria will penetrate clams but found that the resulting metacercariae were dead after four days. It is evident that oligochaetes serve as the natural second intermediate host of the species, and those annelids are eaten in large numbers by the sturgeon. Furthermore, an extensive

examination of oligochaetes from mud bottom areas of the Wabash River has revealed but the one species of metacercaria.

The adult of the metacercaria in question could not be determined experimentally because sturgeons known to be free of *S. manteri* were not available and metacercariae fed to other fishes failed to infect them. As practically all Shovelnose sturgeons examined from the Wabash River were infected, attempts were made to remove the worms by treatment with gentian violet and piperazine, but without success. When infected annelids were force-fed to sturgeons, large numbers of very young worms were recovered from the spiral valve, along with larger ones from previous natural infections, but there were all gradations in size and development. Furthermore, similar gradations occurred in the many worms from a natural infection in one fish that had been held in captivity for 34 days. Thus, the parasites grow very slowly in captive sturgeons, and inability to keep them alive for extended periods made it impossible to utilize the method of superimposing an experimental infection on a natural one and later distinguishing between the two.

Negative results were obtained when metacercariae were fed to other fishes, including the gar, the rock bass, the mud minnow, and a few ictalurid species. Inability to infect catfishes is further evidence that the cercaria in question is not the larva of *Allocreadium ictaluri*. Moreover, failure of other fishes to become infected agrees with the evidently high degree of host specificity of *S. manteri* as indicated by the examination of a large variety of fishes and other animals from the locality over a number of years and finding that trematode only in the sturgeon.

Attempts to demonstrate the life cycle by infecting the mollusk host also were unsuccessful. First of all, it could not be established whether the egg normally hatches in the open or must be eaten by the mollusk. On one occasion, eggs in intestinal mucus stained green with bile pigments were placed in a dish submerged in slowly moving water. The following day nearly all eggshells were empty with the operculum loosened, but no miracidia could be found. From that observation, it was believed that the eggs normally hatch in the open but the experiment was repeated many times without further evidence to that effect. Unsuccessful also were attempts to induce hatching by shaking, both rapid and slow temperature changes, and the osmotic effects of transfer back and forth from water to 0.7 per cent saline. Although no hatching occurred, the larvae survived such treatments. Following the suggestion of Tromba (1954), eggs were placed in 0.85, 3.0, and 10.0 per cent formalin, but no hatching occurred within ten minutes. With Sørensen's phosphate buffer solutions varying from pH 5.3 to 8.0, a few eggs hatched only at pH 6.5 but the miracidia died quickly, partly extruded from the eggshell or lying close to it. Finally, hatching was not induced by mixing eggs with the body fluids of *Pleurocera acuta*, *Campeloma rufum*, or *Goniobasis livescens* or by leaving them in water with much organic debris, a

method that the writer found effective in inducing eggs of *Allocreadium* species to hatch.

Embryonated eggs fed to *Pleurocera acuta* of various sizes, *Goniobasis livescens*, *Campeloma rufum*, and *Amnicola limosa* were passed with the snails' feces, often in large numbers, but were almost invariably unhatched. Those snails that passed open eggshells were maintained for a few days to two months in the laboratory and were then cracked and examined but no stages were found that could be attributed to experimental infection.

Although attempts to complete the life history of *S. manteri* experimentally were inconclusive, circumstantial evidence indicates that the cercaria and metacercaria under consideration are larval stages of that species. In the first place, there is complete morphological agreement in respect to the digestive and excretory systems, eyespot pigment, and body spination. Furthermore, the characteristic excretory concretions of the cercaria are retained through the metacercarial stage and were seen in young adults from naturally infected sturgeons. A biocellate cercaria is established by the remnants of eyespots in the adult and that fact rules out of consideration as the larval stage most of the freshwater cercariae. The remaining ones, i.e., those with eyespots, are of but a few types in fresh water (monostomes, amphistomes, opisthorchioid larvae, ophthalmocephid cercariae, and a few furcocercous and gymnocephalous species), for nearly all of which the general life history and the systematic group to which the adult belongs are rather well understood. On that basis, all of the biocellate cercariae known to develop in Wabash River mollusks except the one described by Seitner (1951) can be excluded as the larva of *Skrjabinopsolus manteri*. Further circumstantial evidence is the correlation between the presence and abundance of the various stages in certain localities. Where the cercaria, metacercaria, and adult were sought, all were either present or absent in a given locality and if present, their relative abundance is roughly what one would expect of stages belonging to the same life cycle.

STAGES IN THE LIFE CYCLE OF *SKRJABINOPSOLUS MANTERI* (Measurements in millimeters)

ADULT

The description of *S. manteri*, as given by Cable (1952), is supplemented by the writer's observations on the excretory system. In young adults (Fig. 14), it is very similar to that system in *D. inflata*, as described by Cable and Hunninen (1942). The excretory pore leads into a short, saccate bladder confined to the post-testicular region. The posterior ends of the primary excretory ducts are ciliated and enter the bladder anterolaterally to continue along its internal surface and open near the mid-level. Anteriorly, the ducts extend with convolutions to the level of the cirrus sac, where each receives an an-

terior and a posterior secondary tubule; capillaries from three groups of flame cells join each secondary tubule and, as in *D. inflata*, are not dichotomous in arrangement within the flame cell groups. One flame cell of the posterior-most group is considerably larger than others of that group. The maximum number of flame cells seen in young adults is given in the formula $2 [(3+7+14) + (11+12+8)]$ but increases with growth of the worm. In very old worms, the excretory tubules and capillaries are delineated by a pigment which is distinct in both living specimens and whole mounts.

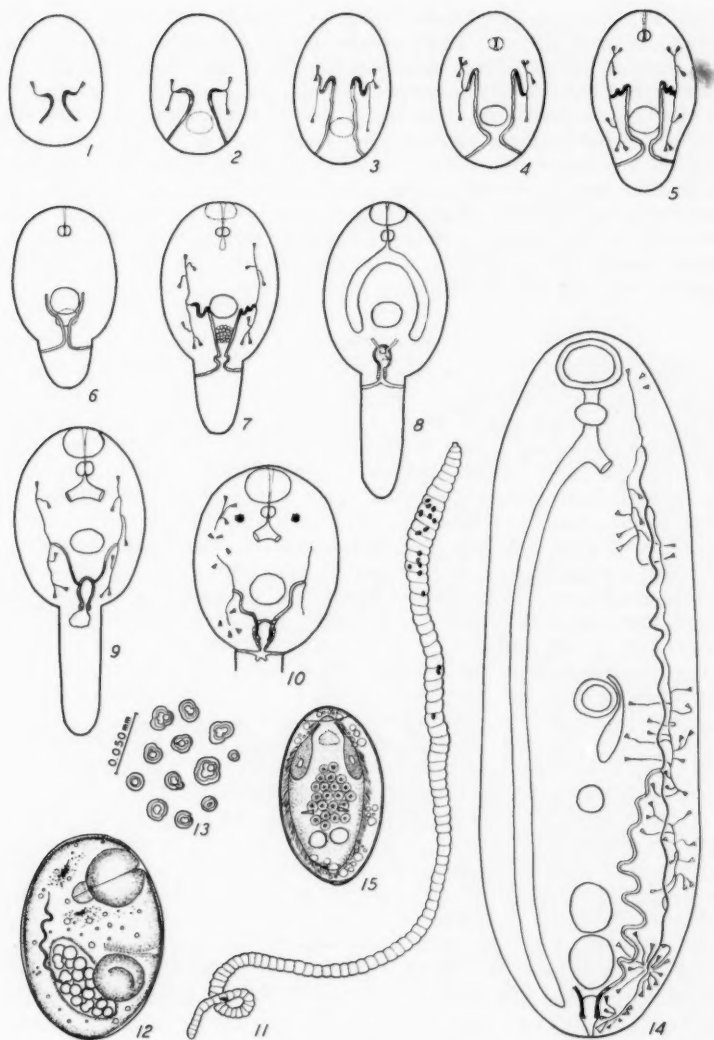
EGG AND MIRACIDIUM

The eggs freshly laid by adults placed in 0.7 per cent saline measure 0.043-0.051 by 0.023-0.026; the shell is yellow, operculate, and has a small antopercular knob (Fig. 15). Certain details of the miracidium were observed through the eggshell. A cephalic gland with a distinct nucleus occurs on each side; it is variable in length but always pre-equatorial. An eyespot is lacking. The two flame cells lie near the midlevel, among a group of over a dozen germinal cells. Commonly observed were two larger vacuole-like structures, possibly excretory reservoirs. Cilia cover the entire surface but are inactive unless pressure is applied to the egg.

CERCARIA

The description of the cercaria given by Seitner (1951) is supplemented here to include the embryology of the excretory system because of its significance in La Rue's (1957) scheme of classification.

Development of the excretory system begins in the germinal ball with the appearance of a pair of flame cells, each with a duct containing a patch of cilia but apparently not opening to the surface (Fig. 1). By the time that the primordium of the ventral sucker appears in the posterior half of the embryo (Fig. 2), there are two pairs of flame cells which beat more slowly than the ciliary patches, and the collecting ducts open posterolaterally. Somewhat later (Fig. 3), there are two relatively large anterior flame cells and a smaller posterior one on each side and the ciliary patch is limited to the recurrent anterior end of the primary collecting duct. As the anterior flame cells increase to three per side (Fig. 4), the primary ducts converge posterior to the ventral sucker and the outline of the pharynx is seen. With elongation of the embryo (Fig. 5), the number of posterior flame cells increases to three on each side. The primordium of the bladder epithelium (Fig. 6) appears posterodorsal to the ventral sucker by the time the tail bud is evident. The excretory ducts posterior to the sucker come very close together to extend into the tail bud and then diverge to open laterally a short distance from the body-tail furrow. With elongation of the tail and appearance of the primordium of the oral sucker (Fig. 7), the excretory ducts form a small lateral convolution near the furrow and



Figs. 1-15.—1-10. Embryology of the excretory system of the cercaria that probably is the larva of *Skrjabinopsolus manteri*. 11. Location of metacercariae in an experimentally infected oligochaete. 12. Ten-day-old metacercaria. 13. Excretory concretions from bladder of 16-day-old metacercaria. 14. Excretory system of young adult *S. manteri* from a natural infection. 15. Egg and miracidium of *S. manteri*.

then fuse to form the bladder (Fig. 8) at about the time that the intestinal ceca appear. Without the flame cell number increasing, the bladder then becomes distinctly epithelial with the ciliary patches of the ducts immediately anterior to it (Fig. 9). An atrium forms in the anterior part of the tail and the primary excretory pores disappear. When eyespot pigment is apparent (Fig. 10), the ciliated ends of the ducts extend into the bladder, the number of flame cells increases, and a secondary excretory pore forms at each side of the body-tail furrow. With further development, the flame cells increase to the number observed in emerging larvae and concretions appear in the bladder. The cuticular spines do not develop until shortly before emergence.

METACERCARIA

Naturally infected annelids were found in the Wabash River at Lafayette and Covington, Indiana. Metacercariae in them were never further developed than those of eighteen-day experimental infections and were mostly in the region of the genital organs (Fig. 11). In one case, a reddish-brown secondary cyst wall was seen, but in general there is very little host tissue response. Several species of oligochaetes, mainly tubificids, serve as natural hosts. Each worm usually contained 1-4 cysts, but 17 were seen in one from Covington.

When oligochaetes are exposed to infection, cercariae may begin to penetrate them almost immediately or may crawl about on the surface for a time but not evidently seeking a particular site to enter. Five to ten minutes are required for penetration; decaudation occurs at the end of the process. Thereafter, the metacercaria migrates at random for two hours or longer, stopping occasionally as if about to encyst but then moving further to do so.

The cyst (Fig. 12) is oval, measures 0.160-0.260 by 0.087-0.110, and does not change appreciably in size with age although its primary wall increases from about 0.001 to 0.004 in thickness by the eighteenth day. The comparatively little development of the metacercaria within the annelid is confined largely to a slight increase in the size of the suckers and pharynx, less vacuolation of the parenchyma, dispersal of the eyespot pigment, and growth of the cuticular spines to a length of up to 0.005 as the entire body becomes spinose. The excretory concretions of the cercaria (Fig. 13) are retained with little change except in size and are composed of concentric layers of a substance that dissolves in weak hydrochloric acid.

DISCUSSION

Species of the genera *Skrjabinopsolus*, *Deropristis*, and *Pristicola* undoubtedly form a natural group, the Subfamily Deropristiinae Cable and Hunninen, 1942, whose family status has been in dispute. Most recent authors have assigned those genera to the Family Acanthocolpidae (Skriabin, 1954; Bykhovskii and Dubinina, 1954; Dawes,

1956; Yamaguti, 1958), although *Deropristis* had been excluded from that family by Cable and Hunninen (1942), a view accepted by Caballero (1952) and reiterated by Cable (1952, 1955). Adults of the Deropristiinae, however, differ from genera of the Lepocreadiinae and Homalometrinae in the extent of the uterus and vitellaria and in spination of the cirrus and metraterm. On the basis of differences in adult morphology, Skriabin (1958) reversed his earlier view (1954) and removed the genera *Deropristis*, *Pristicola*, and *Skrjabinopsolus* from the Acanthocolpidae, erecting for them the Family Deropristidae. That conclusion has been reinforced by the writer's studies on the embryology of the excretory system of acanthocolpid and lepocreadiid cercariae (Peters, in press) as well as of the species just considered and believed to be the larva of *S. manteri*. All three differ with respect to the location of the primary excretory pores.

Skriabin (1958) did not include in the Deropristidae the genus *Cestrahelminis* Fischthal, 1957, which has more in common with that family than with any other group but differs from the other three genera to the extent that it is considered to represent a distinct subfamily. For that reason the family is redefined and divided into subfamilies as follows:

Family Deropristiidae Skriabin, 1958, emend.

Diagnosis.—Distomes with spinose cuticle, spines sometimes locally enlarged to form patches or a ventrally interrupted collar near anterior end but not adjacent to mouth. Cercarial eyespot pigment present. Mouth subterminal, pharynx and esophagus present, ceca extend at least to level of testes and usually beyond. Excretory vesicle saccate, with posterior pore; flame cells, where known, in three anterior and three posterior groups on each side. Genital pore at edge of ventral sucker, median or displaced to left. Cirrus sac with spiny cirrus, pars prostatica, and saccate seminal vesicle that is usually bipartite. Testes two, well within hindbody. Ovary pretesticular; independent seminal receptacle and Laurer's canal present; vitellaria not extensive, between level of pars prostatica and post-testicular space, usually not reaching posterior testes. Uterus extends posteriorly at least to level of anterior testis and may fill hindbody; metraterm distinct, with very small to prominent spines; eggs moderately numerous to numerous. Adults in intestine of marine and fresh-water fishes. Cercariae biocellate, stylet lacking in known ones; bladder epithelial but not with prominent gland-like cells, large concretions present; primary excretory pores, where known, just posterior to body-tail furrow. Cercariae develop in simple rediae in prosobranch gastropods. Includes the subfamilies:

Subfamily Deropristiinae Cable and Hunninen, 1942

Diagnosis.—With the characters of the family. Esophagus short, intestinal bifurcation well anterior to ventral sucker; ceca long, reach-

ing posterior end of body. Genital pore median; seminal vesicle distinctly bipartite; pars prostatica small, tubular.

Type Genus.—*Deroprists* Odhner, 1905; other genera: *Pristicola* Cable, 1952; *Skrjabinopsolus* Ivanov in Ivanov and Murygin, 1937 (Syn. *Pristotrema* Cable, 1952).

Cestrahelminae n. subfam.

Diagnosis.—With the characters of the family. Esophagus long, intestinal bifurcation near level of ventral sucker, ceca not reaching posterior end of body. Genital pore well to left of midline; seminal vesicle not distinctly bipartite; pars prostatica prominent, bulbous.

Type and Only Genus.—*Cestrahelminis* Fischthal, 1957.

The writer examined the type specimen and sectioned material of *Cestrahelminis laruei* and found that what Fischthal (1957) described as the "inner" thick-walled division of the seminal vesicle actually is the pars prostatica and that the seminal vesicle is not distinctly bipartite, as in other species of the Deropristiidae. Careful focusing on the whole mount revealed a slight constriction that indistinctly separates the anterior part with a slightly thickened wall from a thin-walled posterior portion. In the sectioned specimen, however, such a constriction was not evident, although the difference in the wall thickness of the vesicle was apparent, the posterior end being extremely thin and difficult to distinguish from the cirrus sac itself.

The writer concurs with Skriabin (1958) in withholding judgment as to allocation of *Paratormopsolus* Bykhovskii and Dubinina, 1954, until that genus is better known. The posterior extent of the uterus and relatively scanty vitellaria are in agreement with the Deropristiidae but the external seminal vesicle and unarmed cirrus and metraterm are characteristic of the Lepocreadiidae, the family to which the Deropristiidae is most closely related.

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The Lateral-Line System in the Rio Grande Perch, *Cichlasoma cyanoguttatum* (Baird and Girard)¹

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ABSTRACT: The lateral-line system of *Cichlasoma cyanoguttatum* is similar to that of other perciforms but there are many peculiarities. The tubes of the lateralis scales do not make contact with each other but the innervation of the organs in this part of the system is normal. The external morphology and osteological components of the system are described in detail and compared with that of serranids and centrarchids; the text is copiously augmented with illustrations. The lozenge-shaped canal neuromasts are in general like those of sunfishes but much larger. The sensory cells, unlike most of the cells seen in other fishes, bear multiple sensory hairs. All of the supporting cells penetrate to the free surface of the organ and intercellular bridges connect each with the others, thus forming a kind of syncytium.

Cichlasoma cyanoguttatum is the only member of the family Cichlidae known to occur naturally in continental United States. Its range extends eastward from the Rio Grande in Texas as far north as the Rio Colorado near Austin. Material for this study was collected from the Blanco River, 25 miles northwest of San Marcos and from San Marcos Springs, Hayes County on July 14, 1958. Dr. Kirk Strawn of Lamar Institute of Technology, Beaumont, Texas, assisted in the collecting and Dr. G. A. Moore of Oklahoma State University offered helpful criticisms. I am grateful for their assistance.

Several specimens were fixed in PFA₃, one of Allen's modifications of Bouin's fluid, and others in 10 per cent formalin. Three of the formalin-fixed specimens were stained by the alizarin method of Hollister (1934). In addition, four large specimens were packed in dry ice and subsequently disarticulated for bone study. Other formalinized fish were dried by means of jets of air and the canal system injected with India ink. Innervation was determined by gross dissection under the lens of a stereomicroscope. The lachrymal bone was chosen for microscope sections because of its constancy and ease of removal. Material for sectioning was decalcified in two per cent hydrochloric acid, embedded in pyroxylin and cut at five microns. Some sections were stained with iron hematoxylin and others with Mallory's triple connective tissue stain; all were mounted in picrolyte. Measurements were taken by means of a filar micrometer mounted on a compound microscope. Drawings were made with the assistance of a camera lucida.

EXTERNAL MORPHOLOGY

In its external appearance the cephalic lateral-line system of *Cichlasoma* is similar to that of other perciform fishes (Stensiö, 1947;

¹ Contribution No. 301 from the Zoology Department and Research Foundation, Oklahoma State University. Supported by National Science Foundation Grant G-4323.

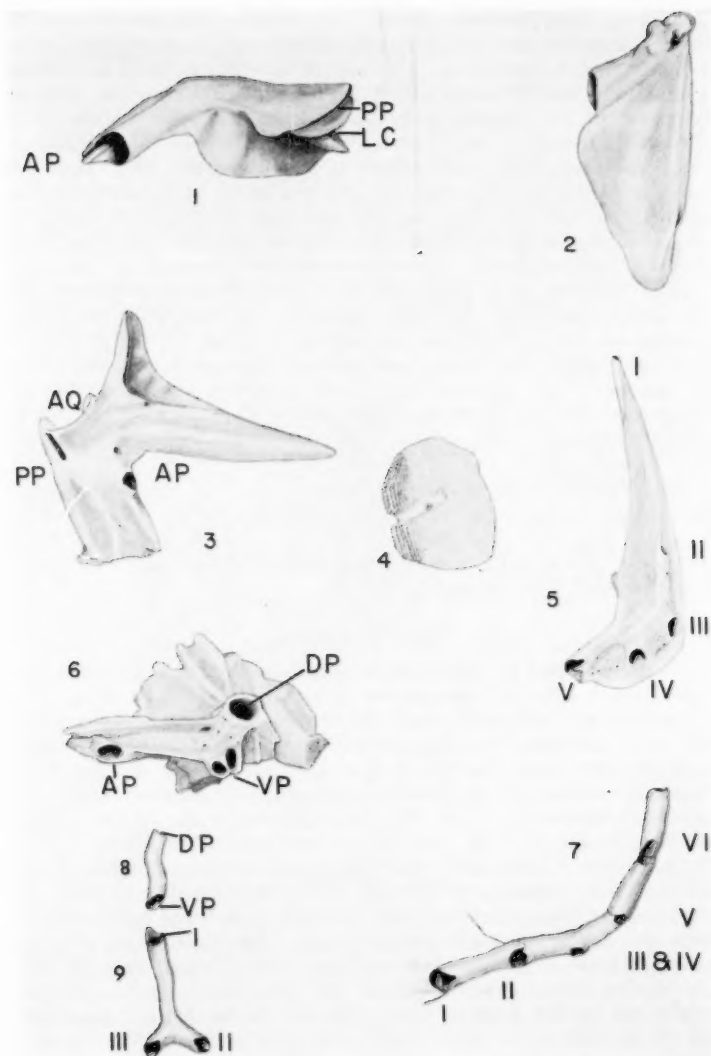
Holmgren, 1942; Moore, 1956). All of the usual components are present, except the supratemporal commissure of some fishes, which is here much abbreviated. The nomenclature employed is modified from Hubbs and Cannon (1935). Throughout the system, with the exception of the secondary branches from the main canals of the lachrymal, frontal, dentary and the preopercle, all of the external canaliculi (branches) arise where two bones meet. The sensory organs contained in the canals are never formed in the branches, but instead form midway between the two ends of a main canal in the case of a simple bone, or midway between two side branches in the case of a compound one.

The coronal pore (MP) of the supraorbital commissure (Fig. 14), in specimens injected with India ink, appears to be an isolated opening on the median line, slightly behind the middle of the eye. In other words, the connection between the pore and the rest of the system is not apparent as it is in sunfishes and serranids. The reason for this will be shown below in the discussion concerning the osseous elements of this system. This commissure is the only canicular connection from one side of the fish to the other.

In sunfishes, with a few exceptions, such as the mud sunfish, *Acantharchus pomotis*, the cephalic lateral-line canals are not covered by scales. On the other hand, in the Rio Grande perch, all of the canals except the supraorbital, infraorbital and the canaliculi (mainly in the skin) are overlaid by scales.

THE LATERALIS

At the junction of the cephalic lateral-line with the lateralis there is a ventrally-directed canaliculus (Fig. 12). This is reminiscent of a similar condition in *Pomoxis annularis*, but in general, sunfishes lack such openings. Posteriad to this point the lateralis is composed of short tubes borne by modified scales (Fig. 4) as in other fishes. However, unlike the centrarchid lateralis, the tube in each scale makes no connection with those of other scales in the series. It is necessary to fill the tube in each scale separately in effecting India ink injections. Observation of cleaned and mounted scales, stained with carmine, reveals small canals open at each end (lacking the side branches that many sunfishes possess) and borne approximately upon the center of each lateralis scale. The neuromasts (Fig. 4) are located about midway between the ends of each tube. In addition to this disjunct arrangement, the lateralis abruptly ends at a position under the sixth or seventh dorsal fin ray from the posterior end of the fin. Two scale rows below this point another series of tubes begins and continues onto the caudal peduncle, where it ends, a few scales anterior to the caudal fin. The upper series overlaps the lower by two pored scales and, in all of the specimens observed, contained 19 tubes; the lower series, which is nearly in a straight line, contained ten tubes. It is supposed that this sort of arrangement is of general occurrence in cichlids since it was also observed in



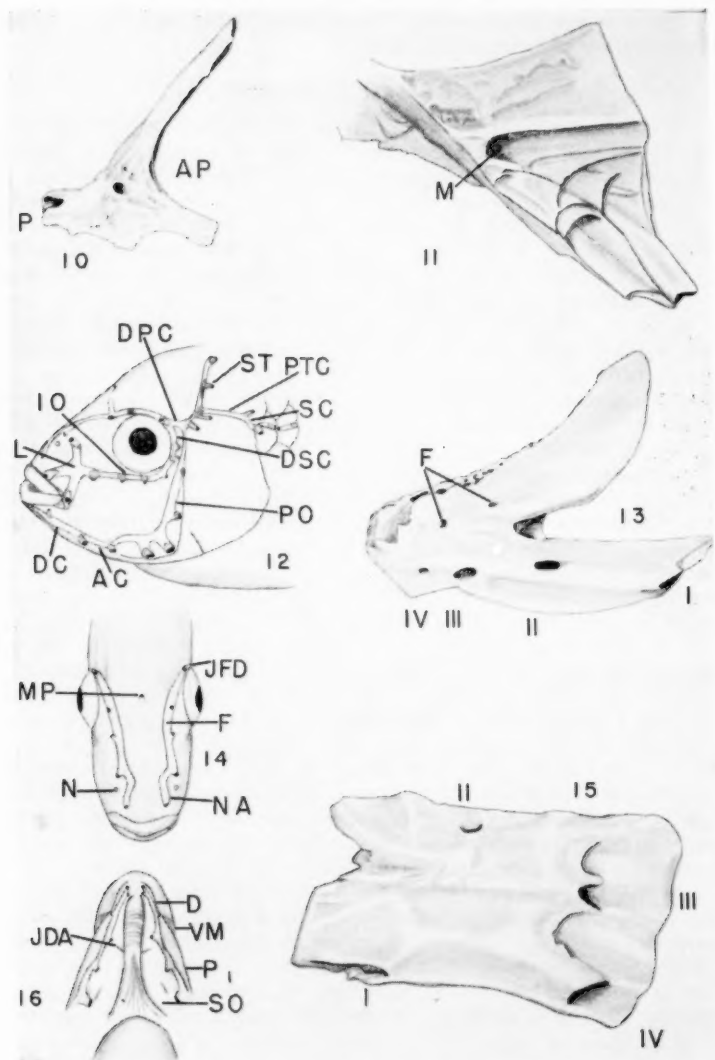
Figs. 1-9.—Lateral line system of *Cichlasoma cyanoguttatum*. 1. Nasal bone $\times 5$. AP, anterior lateral-line opening; LC, chamber under posterior opening; PP, posterior lateral-line opening. 2. Supracleithrum $\times 3.7$. Anterior on right. 3. Articular $\times 5$. AP, as in Fig. 1; AQ, articular surface for anterior facet of the quadrate; PP, as in Fig. 1. 4. Lateralis scale $\times 1$. Anterior on right. 5. Preopercle $\times 2.2$. I-V, lateral-line openings; I, dorsal; V, antero-ventral. 6.

Tilapia nilotica, in the oscar, *Astronotus ocellatus*, and the angelfish, *Pterophyllum eimekei*, all cichlids.

OSTEOLOGICAL COMPONENTS

For proper interpretation of any lateral-line system one must pay particular heed to the bones involved, all of which are of dermal origin. The terminology utilized for the lateral-line bones is that of Harrington (1955). From the trunk the lateral line enters the head region by penetrating the dorsal extremity of the supracleithrum (Fig. 2), which, in a lateral aspect, is roughly acutely triangular. The canal is more capacious posteriorly than anteriorly and is completely enclosed in bone. This arrangement is in general like that of serranids (Woolcott, 1957) and in the Sacramento perch (Dineen and Stokley, 1956) and several other sunfishes (unpublished). The anterior end of the bony canal is in fairly close approximation to the ventral opening of the posttemporal, through which the canal continues its course anteriad. The posttemporal (Fig. 10) is likewise similar to the same bone in serranids and centrarchids except that its posterior end is smooth, whereas in serranids and in *Archoplites* it bears few to many serrae. Another dissimilarity is that the posterior end of the bone bears two pores in sunfishes and serranids; in *Cichlasoma* there is but a single pore. The anterior opening, surrounded by slight hillock of osseous material, delivers the canal to the supratemporal-intertemporal, a small, tubular, inverted Y-shaped bone which is pored at all three ends of the "Y" (Fig. 9). The anterior arm communicates with the dermopterotic and the dorsal extension with the tubular lateral-extrascapular (Fig. 8) which is slightly sigmoid in shape. In sunfishes these two bones are often in the form of open channels. The dermopterotic (Fig. 6) is represented as a blade-like, lateral extension from the pterotic. It is roughly a horizontal-Y in shape and bears three or four lateral-line openings, according to whether the ventral pore is double or single. The dorsal opening communicates with the lower one of the supratemporal-intertemporal; the ventral one or two with the superior end of the preopercle; and the anterior end opens into a common sinus contained in the connective tissue at the postero-dorsal aspect of the eye, where the dermosphenotic and frontal components also communicate (Fig. 12). This bone is similar to that of centrarchids, but it is always completely tubular, whereas in sunfishes it is often seen as an open groove. Furthermore, in sunfishes there are rarely more than two openings, a posterior and an anterior one, the

Dermopterotic and pterotic $\times 5.3$. VP, ventral lateral-line opening; AP, PP, as in Fig. 1. Anterior on left. 7. Infraorbital ossicles $\times 6.7$. II, Jugal III & IV, compound ossicle; V, ossicle 5; VI, Dermosphenotic. 8. Lateral extrascapular $\times 6$. DP, dorsal lateral-line opening; VP, as in Fig. 6. Anterior on left. 9. Supratemporal-intertemporal $\times 6$. I, dorsal lateral-line opening; II, posterior lateral-line opening; III, anterior lateral-line opening.



Figs. 10-16.—Lateral line system of *Cichlasoma cyanoguttatum*. 10. Post-temporal bone $\times 5$. AP, P, as in Fig. 1. 11. Median view, left frontal bone $\times 4.7$. M, median lateral-line opening. 12. Left, antero-lateral view of head $\times 1.7$. AC, articular component of operculo-mandibular canal; DC, dentary component of operculo-mandibular canal; DPC, dermo-pterotic component of the cephalic

communication with the upper end of the preopercle being accomplished from the simple opening in the side of the canal.

From its junction with the dermopterotic to its anterior extremity, the lateral-line passageway borne by the preopercle (Fig. 5) is completely enclosed in bone, except for very short continuations where lateral branches are given off. This canal appears as a slight elevation on about the center of the plate-like body of the preopercle, the upper end being tubular in nature. There are five openings, two terminal and three side-branches. The two anterior-most side branches are surrounded by bone for most of their length and a spongy-appearing osseous material fills in between them. At its anterior end the preopercle is moderately deflected ventrad where it couples with the posterior end of the articular.

In general shape the preopercle (Fig. 5) is not unlike that of serranids and centrarchids, this being about as far as the homology can be carried. The centrarchid preopercular lateral-line canal seldom has the side branches surrounded by bone, these being continued from a slit-like opening to the edge of the bone by connective tissue canaliculi. Furthermore, instead of this particular canal being a solid tube, as it is in *Cichlasoma*, it appears as a simple fold, i.e., as if one had folded a flat piece of bone upon itself, the free edge of the fold being directed caudad. In both Serranidae and Centrarchidae the posterior edge of the preopercle bears conspicuous serrae; these are lacking in *Cichlasoma*.

Slightly in advance of the anterior end of the preopercle the canal enters the articular (Fig. 3), which is shaped about like its homologue in the Centrarchidae. The canal passes downward at a declivitous angle to the point where it leaves the bone to enter the dentary (Fig. 13). The last-named bone is similar to the same bone in sunfishes, being approximately intermediate between a species with a short rostrum, such as *Lepomis macrochirus* or *L. megalotis*, and one with a long rostrum, as *L. cyanellus* or *Chaenobryttus gulosus*. The most obvious difference between centrarchid species and *Cichlasoma* in this respect is the number of lateral-line openings in the bone. The dentary of the Rio Grande perch possesses only four of these openings whereas most centrarchids have five. This is very obvious, even

lateralis canal; DSC, dermo-sphenotic component of the infraorbital canal; 10, infraorbital canal; L, lachrymal component of the infraorbital canal; PO, preopercular component of the operculo-mandibular canal; PTC, posttemporal component of the cephalic lateralis; SC, supracleithral component of the cephalic lateralis; ST, supratemporal (lateral extrascapular and supratemporal-intertemporal) components of cephalic lateralis. 13. Dentary bone $\times 5.2$. F, foramina; I-IV, lateral-line openings. Anterior on left. 14. Dorsal view of head $\times 1$. F, frontal component of supraorbital canal; JFD, junction of frontal canal with dermosphenotic; MP, median pore of supraorbital commissure; N, nostril; NA, nasal component of supraorbital canal. 15. Lachrymal bone $\times 5.3$. I-IV, lateral-line openings. Anterior on right; dorsal above. 16. Ventral view of head $\times 1.7$. D, dentary; JDA, junction of dentary with articular; P₁, preopercle; SO, subopercle; VM, ventral tip of maxilla.

from a cursory observation, for the anterior pores on the jaw of *Lepomis* open in very close approximation to the median suture; in *Cichlasoma* (Fig. 13) this same pore opens some distance behind this point.

The dermosphenotic or suborbital (post-orbital, auct.) number six (Fig. 7) communicates at its upper end with the common sinus behind the eye. This small bone, which rests in a groove on the sphenotic, is in direct contact at its ventral extremity with the dorsal end of a sub-orbital number five (Fig. 7). As is true in the remainder of the suborbital series, at their point of juncture the lateral walls of these two bones are sculptured, i. e., recessed away from each other, to form an oval foramen through which the external canaliculus extends out onto the skin (Figs. 12 and 14). Suborbital three and four are represented by a single bone with a foramen at its center and number two (jugal) communicates with its anterior opening. The jugal then makes connection with the postero-ventral opening of the lachrymal or suborbital number one. All of these bones often possess flat, wing-like processes extending parallel to the head surface.

The lachrymal (Fig. 15) is a fairly large, flattened, parallelogrammatic bone which bears two posterior openings, one dorsal and one ventral, and two anteriorly, dorsal and ventral. The edges of the bone, though often being slightly scalloped, are free of spination. There is a rather deep notch in the posterodorsal margin, and a slight groove, just posterior to the ventral opening, to receive the anterior end of the jugal (Fig. 15). The canal system is only slightly raised above the surface so that on gross inspection the bone appears quite smooth. On closer observation it can be seen that the areas around the canals have been secondarily ossified.

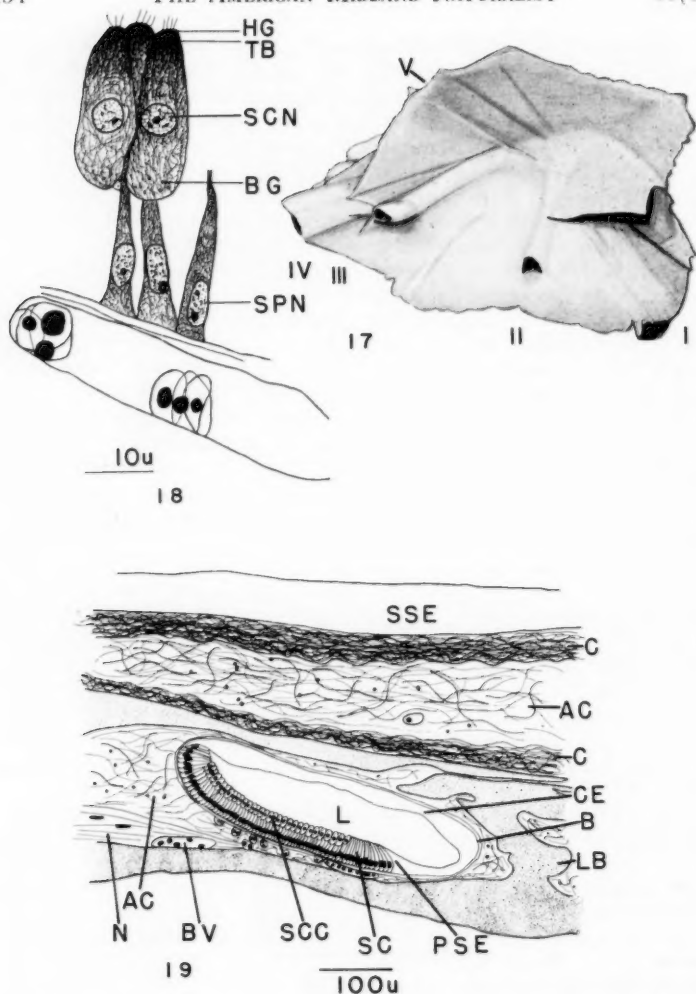
The suborbital series of *C. cyanoguttatum* is like that in some of the sunfishes, i. e., *Ambloplites rupestris*, etc., in possessing six ossicles and in being continuous from the postocular sinus to the lachrymal component. These are, however, several dissimilarities. In all of the specimens of *Cichlasoma* observed, the dermosphenotic, ossicles two, five and the compound three and four were always represented as completely tubular bones, i. e., no open spaces in their walls. In sunfishes their homologues are very often found as simple open channels or with their lateral walls barely touching in one or two small areas. There are, with few exceptions, no special openings for the exit of external canaliculi, the latter simply arising between the ends of the ossicles. The centrarchid jugal is very often lacking, in which case the infraorbital canal is incomplete. The only occurrence of a compound suborbital bone in sunfishes was seen after looking at several hundred individuals. This involved the jugal and suborbital number three in *Micropterus coosae*. However, this single occurrence is considered to be an anomaly and the bone does not in any way resemble the normally-occurring compound structure seen in *Cichlasoma*.

Another obvious difference between sunfishes and the Rio Grande Perch lies in the morphology of the first suborbital or lachrymal. In *Cichlasoma* the bone is elongated in a postero-anterior direction away from the eye and toward the snout, whereas in centrarchids, excluding *Elassoma*, the lachrymal is elongated in a dorsoventral direction and is usually curved on its posterior margin to fit the curvature of the eye. With a few exceptions it is spinous at its antero-ventral edge in the Centrarchidae and its over-all sculpturing is more complex than in the relatively much smoother cichlid bone.

The third lateral-line bearing skeletal component that communicates with the post-orbital sinus is the frontal bone (Figs. 11 and 17). This compact bone possesses five openings: one postero-lateral, one anterior, one above the eye, one near the nostril and one medio-ventral. It is strongly convex in all directions and bears a high crest along its inner edge. This crest is involved in the median suture for its entire length and depth (Fig. 11). The frontal lateral-line canal, after entering the bone from the sinus, progresses directly to the median plane where it bends anteriad, then continues forward until it communicates with the posterior end of the nasal. As it follows this path it gives off two branches, both completely enclosed in bone. One of these, designated II in Figure 18, is located above the eye, the other, marked III, opens just above the nostril. The latter tube is raised above the surface of the frontal and is supported by mesial and ventral struts of bone. The median opening is placed at the base of the bony crest (Fig. 11) from whence it is continued upward and forward by a groove in the crest. A similar groove occurs in the opposite frontal and when the two crests are in their normal sutured position a coronal tube is formed which opens to the exterior on the median line (Fig. 14). The foregoing explains why one is unable to discern the affinities of this pore from India-ink injected specimens.

There are few similarities between the frontals of *C. cyanoguttatum* and those of serranids or sunfishes. In most of the species of the latter two taxa, observed by this writer, there are only four openings in the lateral line and the canal itself is rather superficially placed on the frontal, its position and conformation being easily seen in injected specimens. In centrarchids there are no branches enclosed in bony tubes such as those illustrated in *Cichlasoma*. In sunfishes the frontal canal is a simple Y-shaped tube, the median arm of which opens near the midline, a similar canal opening from the opposite side of the head. An external canaliculus of connective tissue then arises and opens to form the coronal pore, which is a different situation than exists in *Cichlasoma*. Furthermore, the coronal pore of the Rio Grande perch is directed anteriad; in centrarchids it is directed strongly caudad.

The nasal (Fig. 1), the remaining bone of the lateral-line system, is situated anterior to the frontal and is completely ossified, i. e., there are no gaps in its walls. Its anterior and posterior ends are depressed,



Figs. 17-19.—Lateral line system of *Cichlasoma cyanoguttatum*. 17. Lateral view of frontal bone $\times 4.7$. I-V, lateral-line openings. Anterior on left; dorsal above. 18. Lateral-line sensory cells and associated structures (longitudinal section). BG, basal granule; HG, sensory-hair granule; SCN, sensory-cell nucleus; SPN, sustentacular-cell nucleus; TB, terminal bar. 19. Longitudinal section of the lachrymal bone and one of its contained neuromasts. AC, areolar connective tissue; B, basement membrane; BV, blood vessel; C, dense connective tissue; CE, cuboidal epithelium; L, lumen of lateral-line canal; LB, lachrymal bone; N, nerve; PSE, pseudo-stratified epithelium; SC, sustentacular cells; SCC, sensory cells; SSE, stratified squamous epithelium.

giving the bone an appearance of being bent in the middle, and the anterior half is deflected laterad, its tubular portion resting on the curved, plate-like component. The posterior opening, slightly raised above the surface of the bone and protected by osseous lamina above, communicates with the anterior-most opening of the frontal. The anterior pore of the nasal opens to the exterior near the snout tip.

As in its other lateral-line bones, the cichlid nasal is unlike that of any sunfish in which it is usually straightly-tubular, sometimes slightly laterally curved, and usually widened posteriorly to receive the canal of the frontal. Its dorsal wall is usually incomplete.

SENSE ORGANS OF THE SYSTEM

The formation of the lateral line must be completed at a relatively small size in this fish, because all of the canals were completely formed in a specimen 26 mm in standard length. As external neuromasts were not noted the following discussion will concern the neuromasts enclosed in canals.

The canal organ (Fig. 19) of *Cichlasoma* has the same general appearance of many other fish species (Moore, 1956; Moore and Burris, 1956) and is quite like that of most centrarchids (unpublished). The organ is a lozenge-shaped body, averaging $409.0\ \mu$ ($371.0-447.0$) in diameter, situated on the floor or proximal wall of the lateral-line canal, according to the location of a particular canal. The lateral-line tube enclosed by the bony housing is made up of a homogeneous substance which stains pale blue with Mallory's triple stain. Consequently, it is assumed that this substance is a type of connective tissue. This connective-tissue canal, which averages $507.4\ \mu$ ($500.5-514.3$) in diameter, is supported on all sides by loose areolar connective tissue in the bony canal (Fig. 19), the latter varying from 762 to $830\ \mu$ in diameter. The connective tissue tube is actually nothing more than the basement membrane of the epithelial cells lining the canal.

The neuromast consists of two types of cells (Figs. 18 and 19): the sustentacular cells and the sensory cells. The last named cells are completely surrounded by the supporting cells, their bases not touching the basement membrane, and are slightly depressed below the surface of the neuromast so that the organ is thicker in the region adjacent to the sensory area than at its center. The sensory area occupies approximately 55.5 per cent of the total surface area of the organ and averages $227.0\ \mu$ ($202.0-259.7$) in diameter. Typically (Fig. 18), the sensory cells are tenpen-shaped and measure $8.4\ \mu$ ($6.7-9.9$) at the base and $5.4\ \mu$ ($4.2-6.2$) at the apex. They are decidedly polarized, staining much more intensely at their apices than elsewhere. Apically, these cells bear from three to five sensory bristles or hairs, each of which is in contact with a minute, basophilic, blepharoplast-like granule located just beneath the cell membrane. The "hairs" average $2.18\ \mu$ ($1.7-3.2$) in length. It is usually stated (Sato, 1955; Bunker, 1897; Daget, 1949; and others) that each

sensory cell bears a single hair, but in *Cichlasoma*, and in the centrarchids (unpublished) thus far observed by me, the sensory hairs seem to be multiple. The nuclei of these cells are round, centrally placed, vesicular and average 5.1μ (4.0-5.9) in diameter. The nuclear walls are irregularly thickened by chromatin deposition and both acidophilic and basophilic nucleosomes, measuring 0.8 to 1.4μ in diameter, may be seen within it.

Near the apex the sense cells, which average 25.6μ (22.0-30.8) in length, proliferate well-developed terminal bars where they come into contact with their neighbors. Some small granules may be seen below the nucleus, but the basal filaments described by Moore (1956) in *Lepomis humilis* were not seen.

The sustentacular cells (Fig. 18) are very tall and slender, averaging 48.9μ (48.3-57.2) in length, with a finely granular cytosome that is lighter in its staining reactions than that of the sensory cells. The nuclei are oval, as is characteristic of such cells, and cause the cell to bulge in their proximity. These oval structures, like the sensory nuclei, are vesicular in appearance, average 3.5μ (2.9-4.2) in diameter, are basally placed, and bear acidophilic and basophilic endosomes 0.7 to 1.3μ (average 0.98) in size. The supporting cells, peripherally located in the organ, measure 2.3μ at their apices, at which point there are usually seen some terminal bars. In the sensory part of the organ these cells (in sections of 5.0μ thickness or less) are seen to penetrate upward between the sensory cells, their pathway becoming slightly tortuous because of deformation by the contours of the hair-bearing cells. A tangential section of the organ shows that at least the apical ends of the supporting cells, and perhaps the sensory cells as well, are connected by intercellular bridges. These same structures have been noted by Moore (1956) in *Lepomis*, Branson in centrarchids (unpublished), and Maximow and Bloom (1944) in several mammalian tissues. In the pigmy sunfish there is some indication that these bridges may extend throughout the length of the cells.

The general lining of the connective tissue canal is of a moderately high cuboidal nature with scattered goblet cells. However, near the neuromast (Fig. 19) this lining assumes a pseudostratified nature and the goblet cells become very numerous.

The cupula, which several authors have noted in other species (Denny, 1937; Dijkgraaf, 1952; and others) was not seen in this study. However, since this structure is easily dislodged, it may have been removed during fixation and/or staining.

Compared with the canal neuromasts in sunfishes, that of the Rio Grande perch is of greater diameter. Across the base of the organ, in the last named species, the average number of cells was found to be 142. The count in a similar area in representative centrarchids is as follows: *Lepomis auritus*, 85; *L. megalotis*, 53-65; *Acantharchus*, 75-80; *Centrarchus*, 85-90; *Chaenobryttus*, 125-135; and *Pomoxis*, 130-135. The cichlid neuromast is also slightly taller

than those of most centrarchids. Otherwise, this sensory structure is quite comparable in the two families of fishes.

INNERVATION

The innervation of the lateral-line organs is accomplished, as in other fishes (Holmgren, 1942; Hyman, 1956; Moore and Burris, 1956) by branches of the Facial (VII), Glossopharyngeal (IX) and the Vagus (X) nerves. Wherever a neuromast occurs, a nervous twig penetrates the bony canal and the connective tissue surrounding the organ; the twig enters the organ at about its basal center and splays out around the bases of the sensory cells. I could not see any indication of an intimate contact between the sense cells and the nervous endings. However, special techniques would be required to demonstrate this. These nervous twigs are myelinated to the point where they enter the organ and appear to lose their sheath at this junction.

Because of the peculiar form of the lateralis, i. e., the conspicuous line on the trunk of the body, some dissections were made to determine the mode whereby the neuromasts of the lateralis receive their nerve branches from the Vagus, which becomes superficial near the middle of the upper one-third of the supracleithrum, from whence it sends branches to the short canal in the post-temporal, supra-temporal-intertemporal, lateral-extrascapular and a long branch, the lateralis Vagus, caudad in the horizontal skeletogenous septum as observed in other species (Rode and Raband, 1926). The latter branch gives off a twig to each neuromast in the trunk line. As the lateralis canal curves dorsal and away from the septum, these branches become progressively longer, then shorter as the line begins to slope back toward the septum. At the junction where the lateralis is interrupted the twigs cease to be formed and take up again where the second line begins. The nerve twigs to the lateral-line organs of the caudal peduncle, however, are quite short because in this region the Vagus lateralis directly underlies the lateral-line canal. It would be informative to study the embryonic development of this portion of the lateral-line in *Cichlasoma*, but this was not possible in this study. As pointed out above, the smallest specimen available was only 26 mm in standard length and its canal system was already completed.

CONCLUSION

Cichlasoma cyanoguttatum is a member of a depauperate fauna in the United States and though it occupies a similar type of habitat, it is obviously not very closely related to the Centrarchidae. From a gross survey of the lateral-line system in the Rio Grande perch it appears that the morphology of this system is nearly identical to its homologue in sunfishes and serranids, the peculiar form of the lateralis canal excepted. Upon closer inspection, especially of the osseous components of the system, it becomes obvious that there are con-

siderable differences between the two last mentioned families and the system in *Cichlasoma* as regards their lateral lines.

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Revision of the Genus *Melanactes*, with a Proposed New Genus (Coleoptera, Elateridae)¹

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ABSTRACT: The present revisional work of the genus *Melanactes* defines the limits of its six species and presents some ideas regarding their relationships. The distribution of this genus is principally in the United States. Three of the species occur throughout the central and eastern part of the country. One species is confined to the central part and another to the East Coast. Finally, one species occurs in south Oregon, California, and northern Baja California (México). One species is placed under synonymy and another is transferred to a new genus herein described, the latter species occurring only in the southern part of Arizona. A key to species is presented, and redescription of all species are made. Some suggestions concerning the phylogenetic position of the genus *Melanactes* and the new genus are also given.

INTRODUCTION

Melanactes is a small genus of the family Elateridae or click-beetles. Adults of the genus are large, black, shiny beetles found in or near woody areas, frequently resting on the bark of tree trunks. Larvae are very rarely collected, and only the larva of *M. densus* has been associated with its adult. Since the life cycle, at least of *M. densus*, is very long, it is unlikely that the larvae of the genus are predaceous. Rather, they probably feed on decomposing woody material.

The genus, endemic to North America, is represented by six species. Previously, eight species were listed but in the present study one of these is assigned to a new genus and another is placed in synonymy.

The classification of the species of the genus *Melanactes* has been in a confused state for a long period of time. As in many genera of Elateridae, its species do not have striking morphological differences; for example, even the male genital organs, which in the majority of beetles provide very useful characters for the separation of species, are essentially uniform throughout the genus. Moreover, no one has previously attempted to study the species critically, using all of the material available in museums and private collections.

The results of the present study have permitted me to make improved definitions of the species as well as to draw conclusions regarding their phylogenetic relationships. In particular, good interspecific differences have been found in the female organs of reproduction. Externally, useful characters include those of the sculpturing

¹ Submitted in partial fulfillment of the requirements for the degree of Master of Science in Entomology in the Graduate College of the University of Illinois, 1960.

and setation of the pronotum and elytra, proportions of the pronotum, and total length.

Acknowledgments.—I wish to acknowledge with gratitude the generous assistance of the following institutions and individuals in providing me with the material and information upon which the present revisionary study is based: American Museum of Natural History, J. C. Pallister; California Academy of Sciences, H. B. Leech; Carnegie Museum, G. Wallace; Canadian National Collection, E. C. Becker; Chicago Natural History Museum, R. L. Wenzel; Cornell University, H. Dietrich; Illinois Natural History Survey, M. W. Sanderson; Iowa State College, J. L. Laffoon; North Carolina State College, W. M. Kulash; Oklahoma State University, W. A. Drew; Ohio State University, J. N. Knull; Purdue University, L. Chandler; University of Arizona, F. G. Werner; University of California (Berkeley), J. A. Powell; University of California (Davis), A. T. McClay; University of Florida, T. J. Walker; University of Illinois; University of Kansas, G. Byers; University of Missouri, W. R. Enns; University of Nebraska State Museum, R. E. Hill; United States National Museum, J. F. Gates Clarke; Utah State University, G. F. Knowlton; Washington State University, M. T. James.

I am very much indebted to M. C. Lane for suggesting the problem, for the loan of material, and for information. I am also indebted to E. C. Becker for his valuable suggestions and for his interest in my work. For the loan of the type specimen of *Pseudomelanactes agrypnoides* I want to thank H. B. Leech. For comparing my material with the LeConte type material of *Melanactes* I am grateful to F. Pacheco.

My study at the University of Illinois was made possible by a scholarship from the Rockefeller Foundation. For their interest in me and their assistance I am grateful to a number of individuals associated with the Foundation, both in Mexico and in New York. In particular, I want to mention D. Barnes, W. W. Gibson, J. J. McKelvey and K. Wernimont.

Finally, I take pleasure in thanking R. B. Selander for his advice and direction in the course of this study.

HISTORICAL REVIEW

The taxon now known as the genus *Melanactes* was first defined by Germar (1843), who segregated *M. piceus*, *M. morio*, and *M. reichei* as a separate division of the genus *Pristiophus* Latreille. It was elevated to generic rank by LeConte (1853) in his revision of the Elateridae of the United States. LeConte included 7 species in the genus, of which 2 were described as new in the same publication. The characters given by LeConte for *Melanactes* are as follows: tarsi provided with a very dense brush of hairs beneath; pubescence not conspicuous above; mesosternum elevated, forming a ridge at the sides of the mesosternal groove; pronotum strongly margined at the sides, with the hind angles strongly carinated at the base, and with 2 teeth in front of the scutellum.

Candèze (1863), in his *Monographie des Elatérides*, placed *Melanactes* in his second group (called *Melanactites*), along with 6 other genera. In 1891 he revised his earlier classification, recognizing 27 tribes. In this new classification the group *Melanactites* was broken up and the genus *Melanactes* was placed in the tribe, *Corymbi-*

tites. This system was followed by Schwarz (1906) in cataloguing the family Elateridae in the Genera Insectorum.

Working only with the nearctic elaterids, Hyslop (1917) modified the classification of the family considerably as a result of his studies of both larval and adult characters. He recognized 4 subfamilies and 10 tribes. He could not determine the precise position of *Melanactes* in his classification because the larva of the genus was unknown to him. However, on the basis of adult characters he was able to assign it to the subfamily Pyrophorinae. This assignment was accepted by Leng (1920) although he placed it in a separate tribe (*Melanactini*) of Pyrophorinae.

Subsequent workers have accepted Hyslop's assignment. More recently, Glen (1950) had the opportunity of studying a larval specimen of *M. densus*. As a result of his study, he assigned *Melanactes* to the pyrophorine tribe Denticollini (=Lepturoidini), although he noted that the larva of the genus is quite distinct morphologically from the other members of the tribe.

The limits of the genus have not changed since LeConte's time. One species (*M. agrypnoides*) was added to the genus by Van Dyke in 1932, but in the present study this species is transferred to a new genus.

CLASSIFICATION

Genus *Melanactes* LeConte

Melanactes LeConte (1853, p. 493).

Description.—The members of this genus are rather large insects, measuring from 15 to 33 mm in length. Their main morphological features are as follows:

Body robust, elongated, subdepressed, shiny or very shiny. Color black or reddish-black, the legs and venter dark red, always a little lighter in color than the rest of the body. Mandibles directed forward. Antennae dark, with the apical segments sometimes becoming reddish-brown. Front depressed, sparsely punctured at the middle and posteriorly, becoming more densely and conspicuously punctured anteriorly and at the sides. Antennae serrate; second segment shorter than the third; these two segments not at all serrate, fourth to tenth segments moderately serrate, more or less alike in shape and in size; eleventh segment slightly longer than tenth and constricted at apex (Figs. 11-13). Pronotum as long as broad (measured at the middle), but generally appearing longer than broad, tapering gradually toward the head, with the widest point at the hind angles; pronotum strongly margined at the sides, the margin fading anteriorly at the middle; carina very prominent; hind angles almost parallel at the tip; basal part of the disc visibly sulcate; punctures variable. Elytra at base as broad as base of pronotum; elytra often broader at apical third than at base, especially in females; striae and interstriae variable, but always more strongly impressed at base and at sides than elsewhere. Scutellum heart-shaped, with pubescence variable. Prosternum vari-

ably punctate; prosternal spine very strong, wedge-shaped, with tip rounded; laterally and apically the spine is expanded to form a ventral shelf; height of spine more or less equal to distance between the fore coxae; surface of spine smooth and shiny. Mesosternum with sides of groove prominently raised, slightly divergent, deflected in front to form a short plate; mesepisterna and mesepimera clothed with yellowish hair of variable density. Metasternum smoother and more shiny than the rest of sternum; mesepisterna usually more distinctly punctate than metasterna. Hind coxal plates gradually narrowing toward metepisterna. Tarsi provided beneath with a dense golden brush of hairs; first segment almost twice as long as second; rest of segments gradually shorter; fifth segment as long as first. Tarsal claws simple. Abdomen finely, uniformly, and shallowly punctate.

Male genitalia (Figs. 5-8) with aedeagus elongate-triangular; parameres each with a large tooth laterally near apex, and with three or four setae at apex; basal piece quadrate.

Female genitalia (Figs. 14, 15, and 17) with a large bursa copulatrix, which has two or four heavy rows of spines internally; colleterial glands absent; two accessory glands present near anterior end of bursa copulatrix; spermathecal duct constricted near its junction with spermatheca.

Larva.—The only species of the genus known in the larval stage is *M. densus*. Glen (1950) described this larva from a specimen reared from eggs laid in captivity. It measured 38 mm at 5 years of age. Its main structural features are as follows: dorsum golden brown, venter paler; lateral membranes large, creamy white; caudal notch large, transverse; urogomphi short, robust, bifid; tergal prongs corniform, with sharp, upturned tips; outer prongs three or four times as long as the inner ones.

Discussion.—There is a sexual dimorphism in body size in the species of *Melanactes*. Generally speaking, females are larger than males and more robust in appearance.

The male genitalia are fairly similar in all species. The female genitalia exhibit some interspecific differences, among which the most useful are the number and arrangement of the rows of spines in the bursa copulatrix.

The type species of *Melanactes* is *M. densus* LeConte, as designated by Hyslop (1921).

Key to Species of *Melanactes*

1. Oregon, California, and Baja California Norte; surface of the scutellum without hairs; pronotum quadrate, coarsely and densely punctate, the punctures becoming confluent anteriorly and laterally; elytral surface shagreened throughout (under high magnification) *densus*
Central and eastern United States; scutellum with hair on the surface; without the above combination of characters 2
2. Pronotum finely and uniformly punctate, each puncture bearing an appressed seta which is at least as long as the distance between punctures; pronotum with sulcus well marked at basal third and with a distinct im-

pression on each side at base of hind angle, parallel to carina; form narrower and more elongate than in other species; bursa copulatrix with two rows of spines (Fig. 17); extreme eastern and southeastern United States (Mississippi to Georgia, north to Maryland and Pennsylvania)

.....*reichei*
Pronotum more irregularly punctate, without setae or with very minute erect ones; pronotal sulcus and impressions weakly marked to obsolete; form more robust 3

3. Elytral striae at base well-marked, on disc not canaliculate but represented only by a row of shallow small punctures; interstriae flat, feebly rugose, and therefore very shiny; bursa copulatrix with four rows of spines; the spines very numerous (Fig. 15)

.....*piceus*
Elytral striae canaliculate and well-marked for their entire length; interstriae feebly to strongly convex 4

4. Elytral striae deep, with deep punctures; interstriae strongly convex; bursa copulatrix with two rows of spines.

.....*morio*
Elytral striae shallower; interstriae feebly to moderately convex; bursa copulatrix with four rows of spines 5

5. Pronotum flattened (lateral view), appearing longer than broad; elytral interstriae nearly flat; bursa copulatrix with relatively few spines in the median pair of rows; central, and central eastern United States; allopatric with *consors* (see Fig. 3)

.....*puncticollis*
Pronotum convex, appearing more nearly quadrate; elytral interstriae moderately convex, deeper punctures on the striae; bursa copulatrix with numerous spines in the median pair of rows (much as in *piceus*); Kansas and Oklahoma.*consors*

Melanactes densus LeConte

Melanactes densus LeConte (1853, p. 494).

Melanactes schaumii Candèze (1865, p. 14).

Description.—Male. Length 17.5 to 24.5 mm; width 4.5 to 7.5 mm. Color black or reddish black, not very shiny. Head densely punctate at sides. Antennae with the serrate segments slightly longer than wide about two-thirds as long as pronotum (from apex to tip of hind angles). Pronotum slightly longer than wide, slightly convex; posterior angles not at all divergent; carina very broad and well raised, sides more or less parallel, rounded from the anterior third to front; disc moderately densely and finely punctured, the punctures becoming confluent and larger on the sides and very dense anteriorly; sulcus obsolescent or obsolete. Scutellum with surface glabrous except for some scattered yellowish hairs on the sides. Elytra feebly shiny; striae indicated only by rows of punctures that are separated from each other by approximately twice their diameter; intervals flat, the entire surface shagreened (under high power). Venter more shiny than dorsum. Proepisterna heavily punctate. Metasterna finely and shallowly punctate. Genitalia (Fig. 7) proportionally broader than in the other species but otherwise morphologically identical.

Female. Length 18.5 to 27.0 mm; width 5.5 to 8.5 mm. Pronotum very often as wide as long. Genitalia (Fig. 17) with two rows of spines in the dorsal part of the bursa copulatrix and a narrow row on each side.

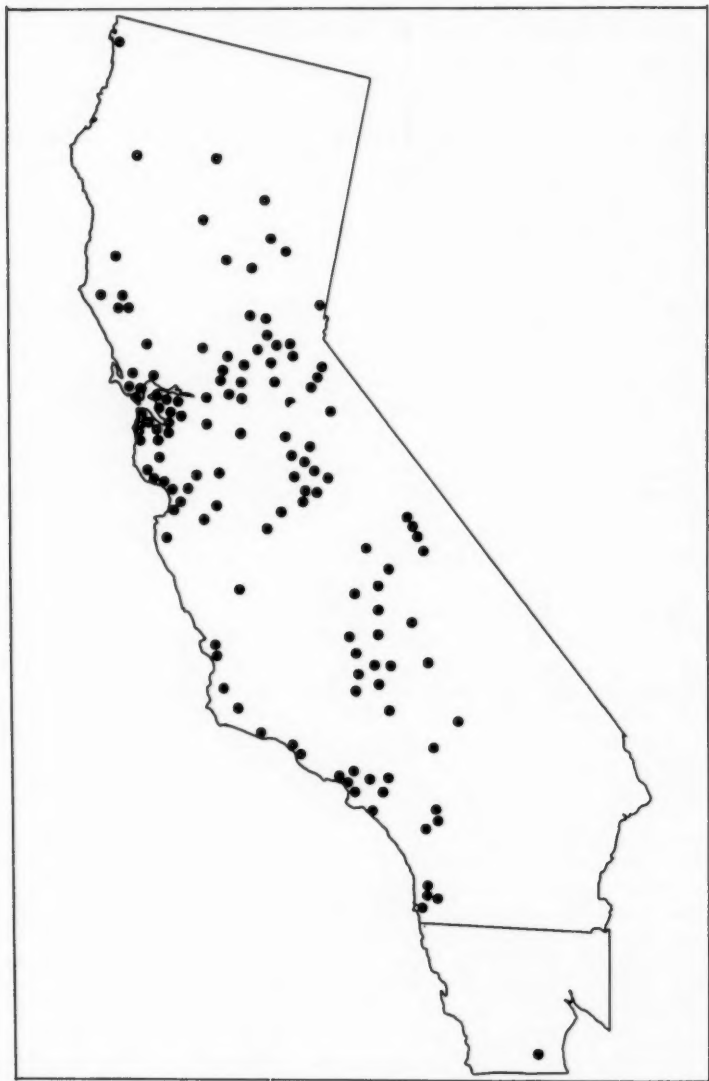


Fig. 1.—Geographic distribution of *Melanactes densus* in California and Baja California Norte.

Distribution.—As can be seen in Figure 1, *M. densus* occurs in California and the extreme northern part of the peninsula of Baja California. In addition, I have seen a single specimen, without precise locality data, from Oregon. In California the species occurs throughout the state except that it avoids the Central Valley and the Mojave Desert.

The species has been collected from late February to early August, but mainly in April, May and June.

MEXICO: BAJA CALIFORNIA NORTE: San Pedro Mártir Mountains, 1.

UNITED STATES: CALIFORNIA: State label, 28; Ahwahnee, 1; Alameda, 1; Alameda Co., 2; mountains back of Alma, 1; Alma, Santa Clara Co., 1; Alpine, 1; Arpa, San Mateo Co., 1; Arroyo Seco Camp, Monterey Co., 4; Bass Lake, Madera Co., 1*; Beatrice, 1; Berkeley, 14; Big Pine, Inyo Co., 11*; Big Trees, Calaveras Co., 1; Bolinas, 1; Boonville, 1; Butte Creek, Butte Co., 6; Caliente, Kern Co., 1; Calistoga, 1; Camino, Eldorado Co., 2; Carmichael, 1; Casalonga, 1; Castle Rock, Shasta Co., 1; Chester, Plumas Co., 2; Chicago Park, 1; Chile Bar, Eldorado Co., 1; Chino Canyon, 1; Chiquito, Madera Co., 1; Claremont, 5; Clarksburg, 2; Clear Creek, San Benito Co., 1; Clear Lake, Lake Co., 1; Coalinga, Fresno Co., 1; Colma, 1; Coloma, 2; Contra Costa Co., 1; Cottonwood Creek, Kern Co., 4; Courtland, 1; Cypress Ridge, Marin Co., 1; Danville, 1; Davis, 9; Dos Palos, 1; Eldorado Co., 2; Fairfax, Marin Co., 1; Fair Oaks, 2; Folsom, 1; Fresno, 3; General Grant National Park, 1; Glen Ellen, 1; Grass Valley, 1; Groveland, 2; Half Moon Bay, 1; Havilah, 1; Hayward, 1; Hemet Reservoir, San Jacinto Mts., 1; Hobergs, Lake Co., 1; Holy City, 1; Hot Springs, Tulare Co., 2; Huntington Beach, 2; Independence, Inyo Co., 2; Isabella, 1; Kaweah, Tulare Co., 14*; Kings River Canyon, 3; La Grange, 18; Lagunitas, Marin Co., 1; Lakeside, 1; Lindsey, Tulare Co., 4; Little Lake, 1; Lloyd Mead, 1; Lodi, 2; Loma Linda, 1; Lonepine, Inyo Co., 5; Los Altos, 4; Los Angeles, 4*; Los Gatos, 4; Mariposa Co., 1; Martinez, Contra Costa, 1; Marysville, 1; Mazourka Canyon, Inyo Co., 1; Meadow Valley, Plumas Co., 1; Miami Ranger Sta., Mariposa Co., 3; Michigan Bar, Sacramento Co., 2; Mission Valley, 1; Mohawk, 4; Mojave Desert, 1; Mokel Hill, Calaveras Co., 18; Mokelumne Hill, 2; Moss Beach, San Mateo Co., 2; Murphys, 2; Mt. Pinos, Kern Co., 2; Mt. View, Santa Clara Co., 1; Napa Co., 6; Natama, 1; Nelson Camp, Tulare Co., 1; Nevada City, 5; Northfork, 4; Oak Creek, Kern Co., 1; Oakhurst, Madera Co., 1*; Oakland, 1; Oakland Hills, 5; Orange Valley, 4; Oro Grande, 2; Outlet, 1; Owens Lake, 1; Oxnard, Ventura Co., 2*; Pacheco Pass, Santa Clara Co., 1; Palm Springs, 1; Palo Alto, 2; Paraiso Springs, 1; Pasadena, 2; Paso Creek, Kern Co., 1; Perkins, 2*; Pescadero, 1; Piedmond, 2; Pilot Hill, Eldorado Co., 1; Piris, 1; Placer Co., 1; Pleasanton, 1; Pleyto, Monterey Co., 1; Pomona, 1; Poso Creek, Kern Co., 1; Potwisha, 2; Poway, San Diego Co., 2; Quincy, 4 miles west, Plumas Co., 5; Redwood, 1; Richmond, 1; Riverside, 4; Round M. Giant Forest, 1; Rutherford, 2; Ryde, 1; Sacramento, 8*; Saint Bruno Hill, 3; Salinas, 1; San Anselmo, 1; San Diego, 8; San Francisco, 5; San Jacinto, 1; San Joaquin, 1; San José, 15*; San Leandro, 1; San Luis Obispo, 2; San Mateo, 1; Santa Bárbara, 5; Santa Cruz, 2; Santa Cruz Mountains, 2; Santa Monica Mountains, 1; Santa Paula, 2; Sequoia National Park, 21*; See Can, 5; Shasta Co., 3; Sierra Nevada, 1; Snowline

* Records of this and other species followed by an asterisk were received (*in litt.*) from Mr. M. C. Lane.

Camp, Eldorado Co., 2; Soquel Creek, Santa Cruz Co., 3; Springville, 3; Stockton, 2; Strawberry, 1; Tejon Canyon, Kern Co., 6; Temecula, 1; Tin Rice, Amador Co., 1; Towle, 2; Trinity Co., 1; Trona, 6; Truckee, 1; Tulare Co., 6; Tuolumne Co., 7; Upper Lake, 1; Victorville, 9; Vina, 2; Visalia, 1; Walnut Grove, 3; Walnut Creek, Contra Costa Co., 1; Walker Pass, Kern Co., 2; Warners, 1; Watsonville, 4; Wanona, Mariposa Co., 2; Woody, 1; Yermo, 5 miles north east, 2; Ynez, 1. OREGON: State label, 1.

Discussion.—This species is the most distinct of all the species of *Melanactes*. It differs from the rest in having little or no pubescence, stouter antennae (Fig. 12), and a more coarsely and densely punctate pronotum. In addition, the body surface is less shiny.

M. densus is the only species of this genus that is known in the larval stage (see above).

The type series of *M. densus* consists of 8 specimens in the LeConte collection at the Museum of Comparative Zoology at Harvard. The first specimen, which bears LeConte's golden locality disc (California), is labeled as Type No. 2619; it measures 23 mm in length and 7 mm in width. One specimen has an identification label reading "*Melanactes schaumii* Cand." Candèze (1863) himself recognized *M. schaumii* as a synonym of *M. densus*; his type is deposited in the British Museum of Natural History.

Melanactes reichei (Germar)

Pristilophus reichei Germar (1843, p. 85).

Description.—Male. Length 20.5 to 21 mm; width 5.0 to 5.5 mm. Body elongated, appearing more slender and more depressed than the rest of the species. Color shiny black to dark red-brown. Front with scattered, well-impressed punctures. Pronotum longer than wide, very flat, tapering gradually toward front; sulcus on the basal third well impressed; at base of hind angles a more or less elongate impression is present; surface densely punctate, especially in front and on the sides, covered with tiny appressed setae. Elytra elongate, tapering from middle to apices; striations and punctures distinct; interstriae slightly convex, more distinctly rugulose than in *M. piceus*. Mesosternum and anterior part of metasternum strongly and closely punctate, covered with a pile of yellowish hairs. Abdomen finely and uniformly punctate throughout. Genitalia elongate; parameres more rounded at the tip than in the other species (subtle difference).

Female. Length 21 to 28 mm; width 5.0 to 7.0 mm; generally larger than male. Bursa copulatrix with fewer spines than in the other species, with the lateralmost row of spines on each side reduced to very few spines.

Distribution.—The geographic distribution is shown in Figure 2A. This insect has been collected from April to July.

GEORGIA: Atlanta, 1; Clayton, 1. MARYLAND: College Park, 1; Hyattsville, 1; Jackson's Island, 3; Montgomery Co., 2; Odenton, 1; Plummers Island, 13. MISSISSIPPI: Lucedale, 2. NORTH CAROLINA: Julian*, Murphy, 2; Raleigh, 3; Tryon, 1. PENNSYLVANIA: Jeannette, 1. SOUTH CAROLINA: Clemson College.*

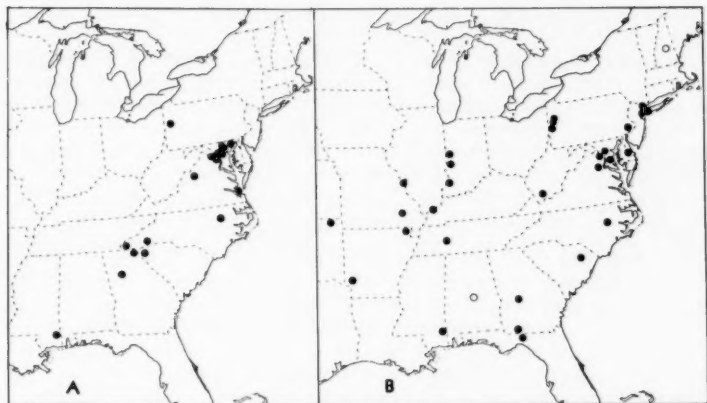


Fig. 2.—Geographic distribution of *Melanactes reichei* (A) and *Melanactes morio* (B).

VIRGINIA: State label, 1; Difficult Run, 1; Glen Carlyn Alex. Co., 2; Great Falls, Fairfax Co., 4; Nelson Co., 1; Phoebe, 1. WASHINGTON, D. C.: 1.

Discussion.—Two extreme variants of this species should be mentioned. These are females collected in Lucedale, Mississippi. They are lighter reddish-brown than usual and have more spines in the bursa copulatrix than in other females. Otherwise, they agree with the other specimens.

I have noticed that the species *Ctenicera aethiops* Herbst has been frequently misidentified as *M. reichei*. The two are similar only in general appearance.

The type is presumably in the Zoological Museum of Berlin.

Melanactes morio (Fabricius)

Elater morio Fabricius (1798, p. 138).

Elater lacunosus Fabricius (1801, p. 224).

Description.—Male. Length 19.5 to 26.5 mm; width 6 to 7.5 mm. Robust, very much of the size and form of *M. piceus*. Pronotum slightly convex; punctures variable, from shallow to deep, sometimes confluent; sulcus visible in the basal third. Elytra having the striae deeply canaliculate, with deep punctures; interstriae very convex, (slightly rugulose) with scattered punctures throughout. Venter as in *M. piceus* but generally with better marked punctures. Genitalia as in *M. piceus*.

Female. Length 22 to 30 mm; width 6 to 9 mm; generally larger than male. Punctures of pronotum sometimes more distinct than in male. Genitalia with two long rows of spines in the bursa copulatrix, more or less as in *M. densus*.

Distribution.—The geographical distribution of this species is

shown in Figure 2B. The species has been collected from May to July.

ALABAMA: State label, 2. ARKANSAS: Hempstead Co., 1; Laurence Co., 1. DELAWARE: State label, 2. FLORIDA: State label, 2; Monticello, 1. GEORGIA: Chakri, 1; Ft. Valley, 2; Thompson Mills, 1. ILLINOIS: Catlin, Camp Drake, 1; Mt. Carmel, 1; Metropolis, 1. INDIANA: Parke Co., 1; Vigo Co., 1. MARYLAND: State label, 1; Beltsville, 1; Jackson's Island, 1. MISSISSIPPI: Lucedale, 1; Meridian, 1. MISSOURI: St. Louis, 1; Williamsville, 4. NEW HAMPSHIRE: State label, 2. NEW YORK: State label, 4; New Windsor, 1; Staten Island, 1; West Point, 3. NEW JERSEY: State label, 1; Da Costa, 1; Fort Lee, 1; New Egypt.* NORTH CAROLINA: State label, 1; Climax*, Julian*, Raleigh, 3. OKLAHOMA: Blue Jacket, 1. PENNSYLVANIA: Fayette Co., 2; Jeannette, 2; Linglestown, 1; Millvale, 1; Philadelphia Co., 1. SOUTH CAROLINA: State label, 2; Florence, 2. TENNESSEE: State label, 1; Benton Co., 1. VIRGINIA: Arlington, 1; Clarendon, 1; Fredericksburg, 1. WEST VIRGINIA: West Sulfur, 1.

Melanactes puncticollis (LeConte)

Pristiophus puncticollis LeConte (1852, p. 68).

Description.—Male. Length 17.5 to 25 mm; width 4.5 to 6.0 mm. Color black to dark reddish black, somewhat shiny. Head sparsely punctate on anterior part, almost glabrous at middle. Pronotum appearing longer than wide; disc flat; sulcus shallowly marked at basal third; more dense on front and at the sides than on disc; some punctures bearing a small erect hair (visible only under high magnification). Scutellum densely pubescent. Elytra elongate; stria well-

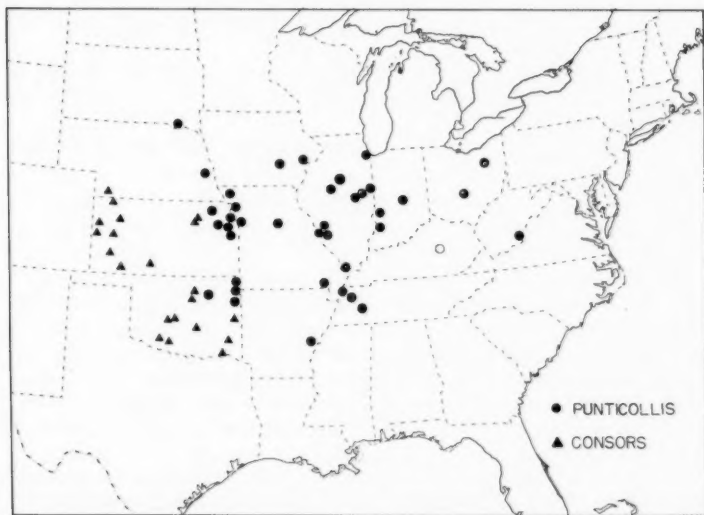


Fig. 3.—Geographic distribution of *Melanactes puncticollis* and *Melanactes consors*.

marked at base, elsewhere only faintly canaliculate, represented by punctures which are separated from each other by their own diameter; first three interstriae flat, the rest becoming very slightly convex; interstriae punctate and to some extent rugulose. Genitalia as in *M. piceus*.

Female. Length 21 to 24 mm; width 5 to 6.5 mm; usually larger than male. Genitalia as in *M. piceus*, except for the short median rows of spines in the bursa copulatrix, which have fewer spines.

Distribution.—The geographical distribution is indicated in Figure 3. Specimens have been collected from late April to August but mostly in June.

ARKANSAS: State label, 9; Prairie Co., 1. ILLINOIS: State label, 2; Alton, 1; Belle Smith Spring, Pope Co., 2; Falling Springs, 1; Goodfield, 6; Havana, 1; Mascoutah, 1; Monticello, 4; Plainfield, 1; Pulaski, 1; Urbana, 5; Vermilion Co., 1. INDIANA: Knox Co., 1; Marion Co., 1; Vigo Co., 2. IOWA: Iowa City, 1; Ames, 1. KANSAS: State label, 4; Douglas Co., 4; Lawrence, 3; Leavenworth Co., 1; Onaga, 3; Topeka, 1. KENTUCKY: State label, 2. MISSOURI: State label, 1; Columbia, 3; Kansas City, 1; Maryville, 1; Saint Joseph, 1; Saint Louis, 4; Webster Groves, 1; Williamsville, 1. NEBRASKA: South Bend, 1; West Point, 1. OHIO: State label, 1; Columbus, 2; Ira, 1; Wayne Co., 1. OKLAHOMA: Ottawa Co., 1; Sallisaw, 1; Tahlequah, 1; Tulsa, 1; Wyandotte, 1. SOUTH DAKOTA: Springfield, 2. TENNESSEE: Dyer Co., 1; Lake Co., 1; Perryville, 1.

Discussion.—This species resembles *M. piceus* but can be separated easily by its smaller size and by the distinctness of the striations of the elytra. It is also very similar to *M. consors*. It can be separated from the latter on the basis of its less convex pronotum and allopatric distribution.

The LeConte material consists of seven specimens, two of which are labeled "Ks." A specimen bearing a label reading "Type No. 2620" is the smallest of the series (length 20 mm; width 6 mm). LeConte gave the type locality as Missouri Territory.

Melanactes consors LeConte

Melanactes consors LeConte (1853, p. 495).

Description.—Male. Length 17.5 to 23 mm; width 5 to 6 mm. Similar to *M. puncticollis*. Head moderately densely and more or less deeply punctate, the punctures at front more numerous and deeper than elsewhere. Pronotum as wide as long; disc convex; surface with a continuous convexity from base to front; sides rounded; hind angles parallel; sulcus barely visible on the posterior third. Elytra broad; striae distinctly canaliculate, with well impressed punctures; interstriae semiconvex, distinctly rugulose. Genitalia as in *M. puncticollis*.

Female. Length 20.5 to 28 mm; width 6 to 8 mm; generally larger than male. Pronotum wider than in male. Genitalia as in *M. piceus*.

Distribution.—The general distribution is shown in Figure 3. The species has been collected from May to August, mostly in June.

KANSAS: State label, 6; Belvidere, Kiowa Co., 1; Decatur Co., 1; Garden

City, 1; Gove Co., 9; Greeley, 1; Manhattan, 1; Riley, 2; Scott Co., 4; Wallace Co., 3. NEBRASKA: McCook, 1. OKLAHOMA: Hinton, 1; Hugo, 1; Kiowa, 1; Norman, 2; Pawnee, 2; Pearson, 1; Stillwater, 1; Wichita National Forest, 4.

Discussion.—This is the smallest species of the genus. It was described from one specimen collected in Nebraska. This specimen, which is in the LeConte collection at the Museum of Comparative Zoology, bears type label No. 2621. It measures 24 mm in length and 8 mm in width.

Melanactes piceus (DeGeer)

Elater piceus DeGeer (1775, p. 162).

Elater laevigatus Fabricius (1798, p. 138).

Pristilophus femoralis Melsheimer (1844, p. 216).

Melanactes procerus LeConte (1853, p. 493) *New synonymy*.

Description.—Male. Length 21 to 28.5 mm; width 5.5 to 7.5 mm. Body robust, subdepressed, color black or dark reddish black, very shiny. Antennae and legs reddish black, somewhat lighter in color than body. Pronotum appearing longer than wide; hind angles slightly divergent; punctures sparse and very shallowly marked, so that the surface appears almost smooth. Elytra as wide as base of pronotum; striae on disc not at all impressed, indicated merely by rows of elongate punctures; striae at sides a little better impressed; all striae finely punctate, the punctures separated from one another by more than their length; interstriae flat, very minutely and indistinctly punctulate; interstrial rugosity feeble. Scutellum covered with a

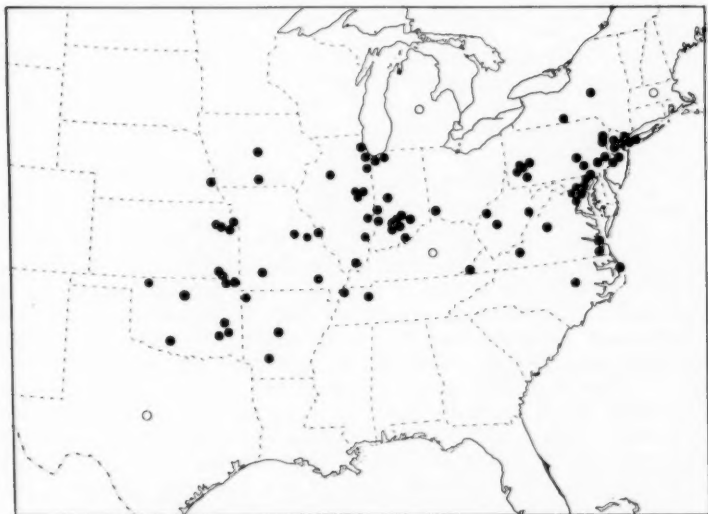


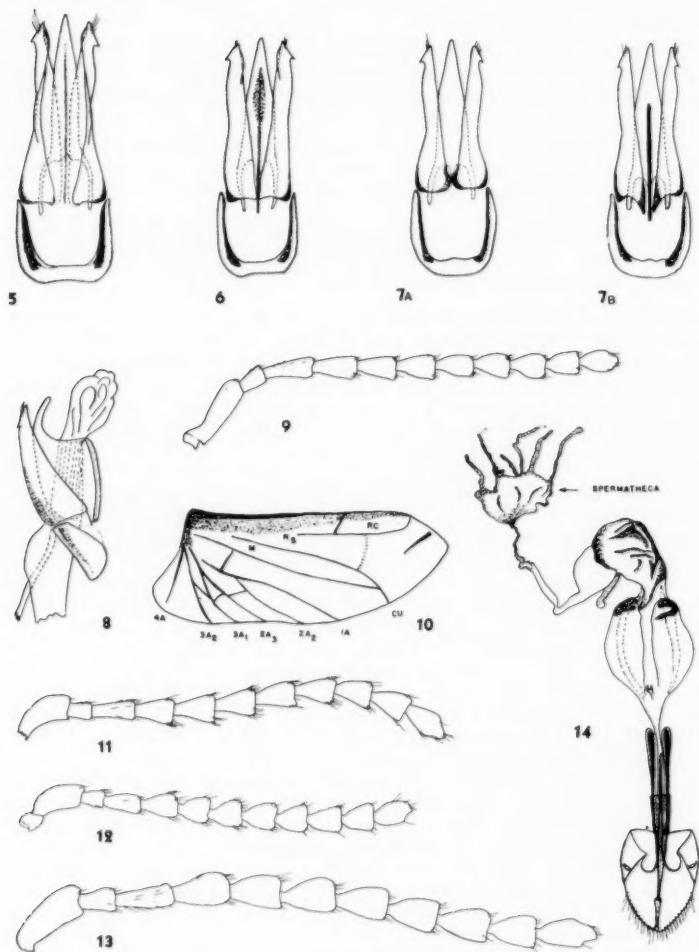
Fig. 4.—Geographic distribution of *Melanactes piceus*.

dense pile of yellowish hair. Mesepisterna and mesepimera covered with yellowish hair. Genitalia (Fig. 5) slightly longer and more slender than the general type.

Female. Length 20.5 to 33 mm; width 4.5 to 9 mm; usually larger more robust than male. Body more heavily punctate than in male; in some extreme variants the punctures of the pronotum become confluent at the sides. Genitalia (Fig. 15) with numerous spines in the bursa copulatrix arranged in a pair of heavy lateral rows running to the front and four dorsal rows, the median pair of which are much shorter than the others.

Distribution.—The general distribution of *M. piceus* is indicated in Figure 4. The species has been collected from early April to August, but mainly in May and June.

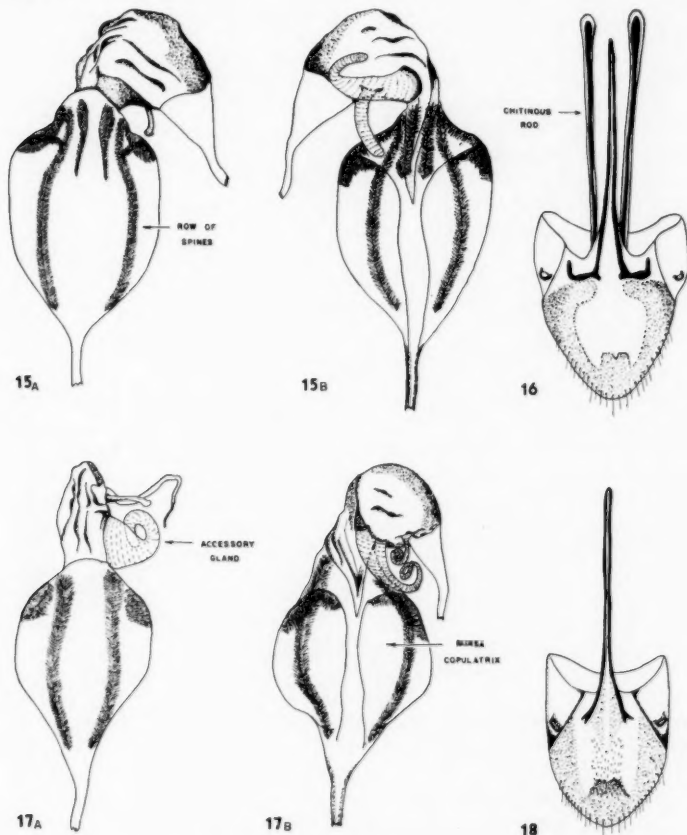
ARKANSAS: State label, 2; Hot Springs, 1; Washington Co., 2. ILLINOIS: State label, 13; Beebe's Woods, east of Crete, 1; Cabelen, 1; Chicago, 3*; Downers Grove, 2; Falling Spring, 1; Galesburg, 1; Homewood, 1; Mahomet, 4; Mascoutah, 1; Monticello, 3; Oakwood, 3; Oblong, 2; Parkersburg, 1; Peoria Co., 1; Pinkstaff, 1; Putnam Co., 1; Saint Joseph, 2; Urbana, 7; White Heath, 2; White Springs, 1; Willow Springs, 16*. INDIANA: Brown Co., 1; Clark Co., 17; Crawford Co., 3; Dune Park, 2; Harrison Co., 1; Henryville, 1; Jacks Co., 1; Jennin Co., 1; Knox Co., 1; Lake Co., 1; Lawrence Co., 1; Putnam Co., 2; Valparaiso, 1; Vigo Co., 1. IOWA: State label, 3; Ames, 5; Carbonado, 1; Leon, 1. KANSAS: State label, 20; Bourbon Co., 1; Douglas Co., 4; Elk City, 1; Lawrence, 1; Leavenworth Co., 2; Montgomery Co., 2; Topeka, 2. KENTUCKY: State label, 3. MARYLAND: State label, 1; Aberdeen, 1; Baltimore, 7; Beltsville*, Bladensburg, 1; Camp Meade*, Great Falls, 1; Lakeland, 1; Montgomery Co., 2; Plummers Island, 1; Wolfsville, 1. MASSACHUSETTS: State label, 4. MICHIGAN: State label, 3. MISSOURI: State label, 4; Cedar Gap, 1; Columbia, 2*; Saint Louis, 3; Willard, Green Co.*, Williamsville, 1. NEBRASKA: Nebraska City, 6. NEW JERSEY: State label, 17; Avenel, 5; Berkeley*, Chester*, Croperill Hill, 1; Englewood*, Englewood Cliffs*, Essex Falls, 1; Fort Lee, 19*; Greenwood Lake, 1; Hillburn*, Hopatcong, 1; Houghton Hill, 2; Montclair, 1*; Moorestown*, Newark, 1; Plainfield, 1; Riverton, 1; Roselle Park*, Snake Hill, 1; South Orange, 2; Springfield*, Summit, 1. NEW YORK: State label, 6; Bear Mounts, 2; Bronx, 3*; Greenwood Lake, 2; Grymes Hill, 2; Long Beach, L. I.*, New City, 1; Orangeburg, 2; Ridgefield, 1; Staten Island, 9*; Van Cortland Park, 1; West Point, 24. NORTH CAROLINA: Julian*, Raleigh, 3; Roanoke Island*. OHIO: Sugar Grove*, Cincinnati*. OKLAHOMA: Alva Okl. Terr., 1; Blue Jacket, 6; Craig Co., 1; Latimer Co., 1; Ottawa Co., 5; Stigler, 1; Stillwater, 4; Wagoner, 1; Wilburton, 1; Wyandotte, 3. PENNSYLVANIA: State label, 4; Abington, 5; Allegheny, 1; Aspinwall, 1; Clarks Valley*, Dunbar, 1; Dauphin Co., 10; Enterline, 1; Fair Oaks, 1; Frankford, 1; Harrisburg*, 1; Hummelstown, 2*; Indiana, Monroe Co., 2; Jeannette, 25*; Linglestown, 1; Millvale, 1; Mount of Holly Springs, 1; Pittsburgh, 25*; Philadelphia, 1; Sciota, 2; Wall, 1; Wind Gap, 3; Wyomissing, 4. TENNESSEE: State label, 2; Benton Co., 2; Deer Lodge*, Lake Co., 1; Perryville, 4; TEXAS: State label, 6. VIRGINIA: Bluemont, 1; Clarendon, 1; Dyke, 1; Falls Church, 6; Glencarlyn Alex., 1; Great Falls, 3; Montgomery Co., 13; Nelson Co., 2; Pennington Gap, 1; Phoebie, 2; Suffolk, 1; Warrenton, 1. WEST VIRGINIA: State label, 1; Athens, 1; Cheat Mountains, 19; Holly Grove, 1; Kanawha Sta., 2; Pocahontas Co., 4; Ripley, 1; West Sulfur, 4.



Figs. 5-14.—Anatomical features of *Melanactes*. 5. Ventral view of male genitalia of *Melanactes piceus*. 6. Ventral view of male genitalia of *Melanactes morio*. 7. *Melanactes densus*. Dorsal (A) and ventral (B) views of male genitalia. 8. *Melanactes* sp. Male genitalia fully distended, showing everted vesicle. 9. Male antenna of *Melanactes*. 10. Hind wing of *Melanactes morio*. 11. Male antenna of *Melanactes reichei*. 12. Male antenna of *Melanactes densus*. 13. Male antenna of *Melanactes piceus*. 14. Female reproductive organs of *Melanactes* sp.

Discussion.—This is the most common and widely distributed species of *Melanactes*. It is easily recognized by its smooth and shiny appearance.

The type locality for *M. piceus* given by DeGeer is "Pensylvanie." According to the description, the type specimen is 26 mm long and 8 mm wide. It is probably in the Riksmuseum of Natural History in Stockholm.

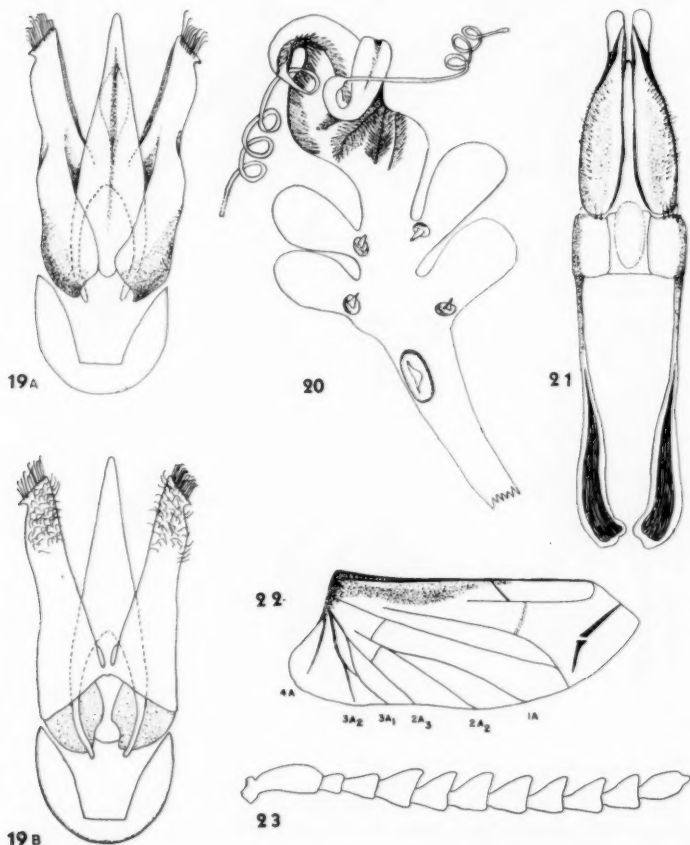


Figs. 15-18.—Female structures of *Melanactes*. 15. Female genitalia of *Melanactes piceus*. A. Dorsal view, showing the four rows of spines in the bursa copulatrix. B. Ventral view, showing also the lateral anterior row of spines. 16. *Melanactes piceus*. Eighth sternite of female and chitinous rods of the genital organs. 17. Female genitalia of *Melanactes densus*. A. Dorsal view, showing the two rows of spines in the bursa copulatrix. B. Ventral view. 18. Eighth sternite of female, *Melanactes reichei*.

The type of *M. procerus*, in the LeConte collection at the Museum of Comparative Zoology (Type No. 2628), measures 33 mm in length and 9.5 mm in width. It agrees with the female of *M. piceus* in all characters.

Genus *Pseudomelanactes*, new genus

Description.—Large, robust. Dull black; antennae and legs reddish black. Head with front slightly depressed, rather coarsely, somewhat closely punctate; mandibles directed downward. Antennae



Figs. 19-23.—Anatomical features of *Pseudomelanactes agrypoides*. 19. Ventral (A) and Dorsal (B) views of male genitalia. 20. Female internal genitalia. 21. Female external genitalia, with chitinous rods. 22. Hind wing. 23. Male antenna.

(Fig. 23) longer than two-thirds of the length of pronotum but not reaching hind angles; second segment small, slightly longer than wide; third, one and a half times as long as second, apically dilated; fourth to tenth broadly serrate; fourth slightly wider than long; following segments gradually narrower; eleventh elongate, constricted before apex. Pronotum from apices of hind angles to apex longer than wide, but appearing more or less quadrate; sides rather broadly arcuate at hind angles, narrowing toward apex; hind angles prominent, distinctly divergent, blunt at apex, carinate; carinae long and close to margin; marginal groove extending but slightly beyond middle, at that point fusing with margin; disc convex, rather coarsely, moderately densely punctate in front, and at the sides; punctures less well-impressed and more separate at middle and behind; sulcus absent; a prominent prescutellar tubercle present. Scutellum subquadrate, with margins well elevated and disc sparsely and finely punctate. Elytra almost twice as long as wide; sides slightly arcuate and gradually narrowed from basal third to apex; disc convex; striae well impressed at base, elsewhere indicated only by a series of fine, moderately closely-placed punctures, which gradually become deeper and more conspicuous from the center to the sides; interstriae flat except at base, rugulose and very finely punctate; humeri rounded and prominent; ninth interstria of each elytron very prominent in front and with a deep groove between it and margin. Anal cell not present in hind wing (Fig. 22). Prosternum coarsely, not closely punctured. Prosternal spine elongate, rod-like, more or less cylindrical, with a pointed tip. Proepisterna more finely and closely punctate than rest of venter. Mesosternum with the sides of the mesosternal groove slightly raised, expanded laterally into two concave plates; margin of mesosternal groove more or less parallel. Epipleura provided with yellow hair at the level of the mesepimera, becoming very sparsely clothed behind it. Metasternum coarsely not closely punctate, very finely punctate at middle. Hind coxal plates narrowing gradually toward metepisterna. Tarsi on the under side clothed with a brush of golden hairs; first segment twice as long as second; other segments gradually shorter; fifth as long as first. Tarsal claws simple. Abdomen uniformly and shallowly punctate.

Male genitalia (Fig. 19) with basal piece rounded; ventral side and tip of the parameres provided with a dense clothing of hairs, curved at the tip.

Female genitalia (Fig. 20) and eighth abdominal sternite (Fig. 21) large, heavily sclerotized; distal part of vagina having a plate-like tubercle; bursa copulatrix membranous, bearing four smaller sharp pointed tubercles located at the base of the four colleterial glands; from this point the bursa becomes more sclerotized and splits into two ducts; one duct (leading to the spermatheca) has two rows of spines running for its length; the other (leading to an accessory gland) is provided basally with a V-shaped row of spines, flanked by an additional row on each side.

Discussion.—The relationships of this genus are discussed below. It contains only a single species, *Melanactes agrypnoides* Van Dyke, which automatically becomes its type species.

***Pseudomelanactes agrypnoides* (Van Dyke) new combination**

Melanactes agrypnoides Van Dyke (1932, p. 446).

Description.—Male. Length 26.5 to 28 mm; width 8 to 9 mm. Large, black, not very shiny beetles. Antennae heavy, not reaching hind angles of pronotum; first three segments scarcely pubescent; remaining segments densely covered with short yellowish hairs (visible only under high magnification). Pronotum with disc more shiny than elytra, entire surface covered with small setae (visible only under high magnification). Epipleura provided with abundant yellowish hair at the level of the mesepimeron, becoming sparsely clothed toward the metasternum. Genitalia as in Figure 19.

Female. Length 31 mm; width 9.5 mm. Genitalia as in Figure 20.

Distribution.—This species occurs only in the southern part of Arizona. It has been collected from July 10 to September 29. Only seven specimens have been collected of this rare species.

ARIZONA: Gila River at Gerónimo, 2600 ft., Graham Co., August 6, 1948, willow-mesquite-cotton area, W. Nutting and F. Werner, CNHM, 1; Nogales, August 14, 1906, F. W. Nunenmacher, CASC., 1; Santa Rita Mountains, September 29, 1922, Werner collection, 1; July 24, W. J. Chamberlin, Lane collection, 1; Tucson, 2300-2500 ft., July 13, 1915, Wickham collection, USNM, 1; Wickenburg, Maricopa Co., July 10, 1953, Etta Beer, Lane collection, 1; (Mr. Lane informs me that there is another specimen with the same data in the Beer collection).

Discussion.—Only a single female was available for study. This specimen is larger than any of the males and has the last visible sternite less acute. Otherwise, it is externally like them.

The species was originally described from a single specimen from Nogales, Arizona. This specimen, a male, is in the collection of the California Academy of Sciences (type No. 3193).

PHYLOGENY

Relationships of the Genera *Melanactes* and *Pseudomelanactes*

Although the genera *Melanactes* and *Pseudomelanactes* are both members of the subfamily Pyrophorinae, their relationship to each other is not a particularly close one. *Melanactes* belongs to the tribe Denticollini (=Lepturoidini). *Pseudomelanactes*, on the other hand, is herein assigned to the tribe Pyrophorini.

There are a great number of characters found in adult *Melanactes* beetles that occur also in other members of the tribe Denticollini. The mandibles are typically directed forward. The scutellum is heart-shaped. As in most Denticollini, the mesosternum is reduced to some extent and is not extended to form plates as in the Pyrophorini. The hind wings are like those of other genera of the Denticollini studied (*Ctenicera* Latreille, *Denticollis* Fabricius, and *Elatichrosis*

Hyslop²) in having a crossvein between veins $2A_3$ and $3A_1$, forming the so-called anal (or wedge) cell (Fig. 10). The basal piece of the male genitalia is more or less quadrate in *Melanactes*, as in *Ctenicera* and *Denticollis*. In *Elatichrosis* the basal piece is rounded, as in the Pyrophorini.

The prosternal spine in *Melanactes* is peculiar in that it is wide, very deep, and wedge-shaped. This particular form of spine is found in only one other elaterid available to me for study. This is the Australian *Elatichrosis illita* (Cand.), a single representative of which was received on loan from the personal collection of Mr. Lane.

The characters of the genus *Pseudomelanactes* are most similar to those of the members of the tribe Pyrophorini. The mandibles are directed downward. The scutellum is subquadrate and has elevated margins. The prosternal spine is a long, rodlike process very much like that found in the pyrophorines *Lanelater* Arnett and *Pyrophorus* Illiger. The mesosternum is expanded into concave plates, as it is in the other Pyrophorini studied. The crossvein which closes the anal cell in the Denticollini is not present in any members of the tribe (Fig. 22). As mentioned above, the basal piece of the male genitalia is rounded. Finally, a prescutellar tubercle is found on the pronotum in *Pseudomelanactes* as well as in *Lanelater* and *Pyrophorus*. *Lanelater* is more specialized than *Pseudomelanactes* in having a prosternal groove, while *Pyrophorus* is more specialized in possessing light-producing organs.

The nearest relative of *Pseudomelanactes* that I have seen during my study is an elaterid represented by a single specimen in the Chicago Natural History Museum labeled Tefe (Upper Amazon River), Brazil. This species has all of the characters of *Pseudomelanactes* discussed above and, in addition, is very similar to the genus in the general form of the body and the shape of the pronotum. Unfortunately, I have not been able to identify the specimen.

While I believe that *Melanactes* and *Pseudomelanactes* may be satisfactorily placed in the tribes Denticollini and Pyrophorini, respectively, their phylogenetic relationships to the other members of their tribes remain rather obscure. As intimated in the preceding discussion, *Melanactes* is possibly more closely related to the Australian genus *Elatichrosis* than to *Ctenicera* or *Denticollis*, and there is evidence suggesting that *Pseudomelanactes* is of neotropical origin. Much additional study of both tribes is needed to elucidate the relationships of the genera within them.

Phylogeny of the Species of *Melanactes*

Because of the incompleteness of the fossil record, it is necessary to rely largely on comparative morphology of living species in reconstructing the evolutionary history of the genus. The tribe Denti-

² Although the genus *Elatichrosis* has never been formally included in the tribe Denticollini, there seems to be no reason why it should not be.

collini first appears in the fossil record in the Lower Oligocene, where it is represented by the extant genera *Athous* Eschscholtz, *Limonius* Eschscholtz, and *Cryptohypnus* Lacordaire. In the Miocene there are some elaterid fossils that have been assigned to the genus *Ctenicera* Latreille as well as a specimen from Florissant shales described by Wickham (1908) as *Melanactes cockerelli*. This last fossil seems to have all the external morphological characters of the genus *Melanactes* except that there is some uncertainty as to whether it has the hind angles of the pronotum carinate. If it is not a true *Melanactes*, then it is apparently a very close relative of the genus. Among the living species of *Melanactes* it most closely resembles *M. densus*.

The modern species of *Melanactes* are, in general, very similar to one another morphologically, and it is therefore difficult to find a variety of characters from which to deduce phylogenetic relationships. The most satisfactory arrangement seems to be the one shown in Figure 24. The following discussion is an explanation of the line of reasoning followed in arriving at this arrangement.

In attempting to group the species of *Melanactes* phylogenetically, it is immediately apparent that the two most similar species are *M. puncticollis* and *M. consors*. These two species differ only in the degree of convexity of the pronotum and elytral interstriae. According to the present records, they are strictly allopatric in distribution.

Melanactes piceus shows a close relationship to *M. puncticollis* and *M. consors* in sharing with them the presence of four median rows of spines in the bursa copulatrix of the female genitalia (Fig.

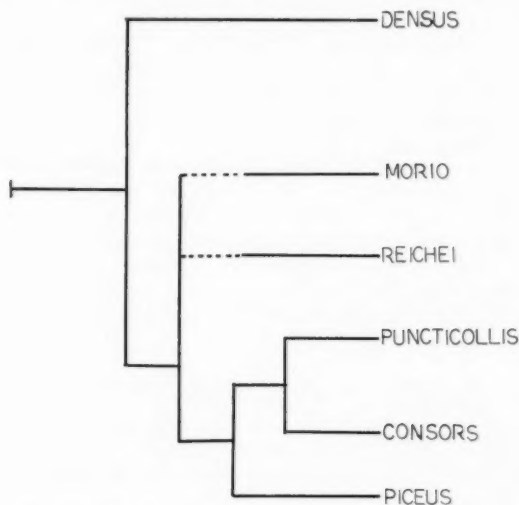


Fig. 24.—Phylogenetic tree of the species of *Melanactes*.

15). It differs from them in that the elytra interstriae are flat and shiny and the striae are shallowly punctate. These elytral characters were probably present in the earliest ancestor of the genus.

The species *M. morio* and *M. reichei* have an obscure origin. They are associated in the tree shown in Figure 24 on the basis of their having only two rows of spines in the bursa copulatrix. Each species has a number of characters which are probably specialized. For instance, in *M. reichei* the body is elongate and there are small appressed setae on the pronotum. In the case of *M. morio*, a great convexity of the interstriae is found and the striae are provided with deep punctures.

Melanactes densus is geographically and morphologically the most distinct species of the genus. It is characterized by a general lack of hair, by flat, canaliculate interstriae, and by the presence of two rows of spines in the bursa copulatrix (Fig. 17). All these characters appear to be primitive for the genus.

It is supposed that *M. densus* evolved from an ancestral population that was at one time widely distributed in the United States and that for some reason was subsequently divided into a western and eastern segment. The western segment of the population gave rise to *M. densus*, which is now confined to the West Coast. The eastern segment produced the remainder of the species of the genus.

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The Lens as an Indicator of Age in the Raccoon

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ABSTRACT: The growth rate of the lens of the eye was studied as a means of determining age in the raccoon. One hundred and nineteen raccoons were studied, including 3 embryos, 18 born in captivity, 42 captured in the wild and kept in captivity for varying periods, and 56 wild animals. Ages of all but those born in captivity were estimated, but these estimates are believed to have an error of no more than ± 2 months. Weights of the dried lenses were used to construct a growth curve which will indicate the month of birth for animals less than 12 months of age, and will estimate the relative age composition of groups of older animals.

There are several useful techniques for determining the ages of dead and live raccoons (*Procyon lotor*) from birth through approximately 8 months of age and for separating males and females less than 1 year of age from those of more than 1 year during the hunting and trapping season (Sanderson 1950 and unpublished). No reliable technique is available for further segregation of raccoons by age after they have passed their first year of life. Lord's (1959) work on the growth rate of the lens of the cottontail rabbit (*Sylvilagus floridanus*) prompted this study of age-defining capacity of the lens in the raccoon.

Acknowledgments.—This is a contribution from Illinois Federal Aid Project No. 56-R, the Illinois Department of Conservation, the United States Bureau of Sport Fisheries and Wildlife, and the Illinois Natural History Survey, co-operating.

Drs. T. G. Scott, C. O. Mohr, and R. E. Yeatter and Barbara A. Chipman read the manuscript and made helpful suggestions. Special thanks are due to Conservation Officers Conrad Foley and Loyd Skinner and to B. J. Verts who supplied many of the raccoons used in this study and to Dr. R. D. Lord, Jr., for helpful suggestions.

METHODS

Raccoons, some born in captivity and others captured in the wild, were kept in captivity varying lengths of time to provide material for this study. Lenses were also obtained from wild raccoons which were live-trapped, ear-tagged, released, and recovered later. Young, unmarked, wild animals were also studied. Ages of all young except those born in captivity were estimated on the basis of a growth curve drawn by using body weights of nursing young born in captivity for the early part of the curve. Later points on the curve were established by plotting weight changes of live-trapped young at subsequent recaptures. The error in these estimates is believed to be no more than ± 2 months (Sanderson, unpublished).

Three males and two females were castrated in order to study possible effects of lack of sex hormones on the growth rate of the lens.

Eyes were removed from a raccoon which was killed a few minutes after birth and from three embryos which were aged by interpretation of data from Llewellyn (1953). The eyes of the raccoons were preserved in 10 per cent formalin. After hardening for several days the lenses were removed, dried in an oven, and weighed to the nearest tenth of a milligram on a micro-torsion balance (see Lord, 1959, for further details of the methods used).

The right and left lenses were weighed in most cases, but there were no significant differences. The dry weight of one lens from each raccoon was plotted to construct a growth-rate curve; however, if the weights of both lenses were available they were averaged, and the average weight was used. Other measurements of the lens were not taken because Lord (1959) found that dry weight gave the best curve in cottontails.

RESULTS

The data (Table I) indicate good correlation between the dry weight of the lens and age up to 12 months (Fig. 1). There is considerable variation as the curve bends between 12 and 20 months of age; after 20 months the curve ascends very slowly.

Initially, males and females were considered separately, but no differences were apparent according to sex. Also, the data were plotted separately for captive and wild animals, but no consistent differences could be seen between 63 captives, including 3 embryos, and 56 wild animals which were studied. There were too few captive and wild raccoons to construct a growth curve of the lens from one group. All but 21 of the captive animals were captured in the wild and were held in captivity for varying lengths of time. Possibly

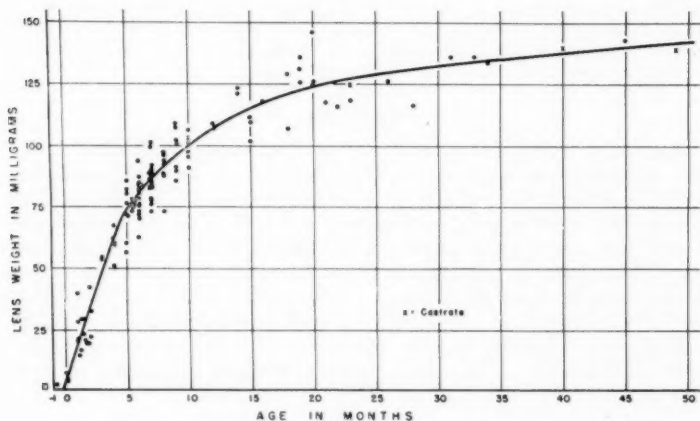


Fig. 1.—The growth-rate curve of the lens based on 119 raccoons of known age.

TABLE I.—The dry weights of lens of raccoons of known ages and estimated ages¹

Age (Days)	Wgt. (mg)	Age (Days)	Wgt. (mg)	Age (Months)	Wgt. (mg)
-21	2.2	180	62.8	9	85.4
- 1	1.8	180	70.1	9	89.4
- 1	2.6	180	71.7	9	92.0
E 0	6.2	180	72.8	9	101.8
E 29	20.2	180	75.4	9	102.2
30	28.7	180	75.6	9	107.6
30	40.0	180	78.1	9	109.3
E 34	14.0	180	80.5	10	91.2
E 34	21.6	180	81.4	10	95.2
E 38	16.7	180	82.4	10	97.3
40	29.0	180	83.8	10	101.6
E 46	23.2	180	83.9	10 ²	102.4
E 49	20.8	180	84.0	10	106.4
49	29.2	180	87.5	12	106.4
E 51	18.5	180	94.3	12	108.4
E 52	19.8	E 206 ²	83.4	14	121.2
60	42.6			14	122.7
E 62	22.3	*		15	102.0
E 65	33.7			15	109.6
90	54.2	7	73.0	15	111.4
90	54.3	7	76.0	16	117.6
120	51.4	7	77.3	18	106.4
120	59.0	7	77.4	18	129.2
120	60.5	7	78.4	19	125.7
120	63.8	7	78.8	19	130.8
120	67.0	7	80.5	19	135.7
150	56.6	7	81.4	20	124.8
150	60.1	7	81.8	20	125.4
150	71.6	7	83.6	20	145.6
150	76.8	7	83.8	21	117.2
150	80.1	7	84.5	22	125.4
150	82.4	7	84.9	23	118.2
150	85.6	7	92.2	23 ²	124.6
E 154	71.9	7	99.8	26	126.2
E 167	68.4	7	101.2	28	116.0
E 168	78.5	8	73.3	31	135.6
E 169	74.0	8	88.4	33	135.6
E 172	75.6	8	88.8	34	133.0
E 172	77.7	8	92.4	40 ²	139.5
		8	94.4	45	142.8
		8	96.5	49 ²	138.4
		8	96.9		

¹ E = exact age, all others are estimated ages. Estimated ages have no more than a ± 2 -month error.

² Castrate.

* (Months).

this fact increased the variability of the data because Lord (personal communication) has found that lenses in wild cottontails grow at a slower rate than they do in captives. Probably contributing to the variance, especially prior to 12 months of age, is the fact that ages were estimated for all of the wild and all but 21 of the captive raccoons. There may be as much as a ± 2 -month error in estimates of the age of raccoons born in the wild. Because lens weights showed considerable variation, especially after 12 months of age, attempts were made to relate body weight and length to lens weight; however, these data gave no better curves than did a direct plot of the lens weights.

Three males and two females were castrated. One male, castrated when 109 days of age, died at 206 days of age. A second male, castrated when approximately 9 months of age, died 14 months later. The third male, castrated prior to 6 months of age, died when 10 months of age. One female, castrated when approximately 26 months of age, died at 49 months of age. The second female, castrated at 17 months of age, died 23 months later. The weights of all their lenses were typical of those of intact animals (Fig. 1).

DISCUSSION

The lens indicates the month of birth for individual raccoons up to approximately 12 months of age. While it may be used to determine the relative age composition of groups over 12 months of age, because of individual variation, it cannot be used to determine the specific age of the animals in the group.

The lens-growth curve of the raccoon is similar to those of the cottontail (Lord, 1959) and the gray fox (*Urocyon cinereoargenteus*) (Lord, in press), except for one important difference. In all three species the data show but little spread up to where the curve bends most abruptly, but then the variation increases and finally decreases again. The ages at which the curves bend seem to occur in all three species at about the time they reach the adult size and, in the raccoon, the bend in the curve corresponds roughly with the time over which the animals reach sexual maturity. Because the raccoon curve is much flatter after this point than that of either the cottontail or the gray fox, it is not possible, from the present data, to determine the year of birth after the first year.

Practically all raccoons in Illinois are 4 to 10, 16 to 22, 28 to 34, etc., months of age during the hunting and trapping season in Illinois, and most fall into the narrower age groups of 6 to 8, 18 to 20, etc., months (Sanderson, unpublished). This fact will reduce the amount of overlap to be found between year classes if this technique is used to analyze the age composition of animals harvested during the open season.

Because there are fewer animals in each succeeding older age group than there are in the younger groups, there are fewer animals

28 to 34 months of age with lenses falling into the 16- to 22-month age group than there are animals 16 to 22 months of age with lenses falling into the 28- to 34-month age group. Thus, individual variation will tend to skew the age composition in favor of the older age groups.

Although only five castrate animals were studied, the fact that the weights of their lenses fall within the groups for intact animals of similar ages indicates that age at attainment of sexual maturity may have little effect on growth rate of the lens.

Other techniques such as those involving the baculum (Sanderson, 1950) and epiphyseal closure (Sanderson, unpublished) are easier and more convenient to use for separating a population into two age groups: those less than 1 year of age and those older than 1 year of age. Epiphyseal closure can also be used in live animals by use of X-rays. However, the lens seems to offer possibilities for separating a population into more than two age groups and for determining the month of birth for raccoons less than 1 year old.

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Notes on the Local Distribution of *Peromyscus leucopus* and *Zapus hudsonius*

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ABSTRACT: The factors influencing the local distribution of *Peromyscus leucopus* and *Zapus hudsonius* were studied in seven habitats (old field, hardwood swamp, coniferous swamp, bog mat, spruce burn, upland hardwood, and grass sedge marsh) in southern Michigan. The environmental factors considered were vegetation type, cover (fallen trees, brush, leaf litter), temperature, food, moisture, and interspecific competition. *P. leucopus* permanently inhabited only wooded habitats (those with trees or shrubs). There was no indication of an avoidance of herbaceous vegetation; there appeared to be a positive response to a tree-shrub type of vegetation. The reason for such a response was not determined. Among the forested areas, an oak-hickory upland was the most favorable habitat. A larger and more stable food supply (acorns and nuts) appeared to be the major factor responsible for the greater abundance of *P. leucopus* in this habitat. Temperature, moisture, cover, and interspecific competition were not important factors in the selection or avoidance of a particular habitat. *Z. hudsonius* was found only in moist situations and was slightly more abundant where there was standing water. Vegetation, temperature, cover, and interspecific competition were not important factors in its local distribution.

During the course of a field study of the local distribution of microtine rodents and shrews in southern Michigan, data were obtained pertaining to the white-footed mouse, *Peromyscus leucopus*, and the jumping mouse, *Zapus hudsonius*. Although the study was not designed primarily for these two species, there was sufficient variation in the habitats to determine the influences of certain factors. Since information concerning the local distribution of small mammals is relatively rare in the literature, it seems advisable to make these data available.

The information presented in this paper has been extracted from a thesis presented in partial fulfillment of the degree of Doctor of Philosophy in the University of Michigan.

DESCRIPTION OF THE STUDY AREA AND METHODS

Study area.—All the work was done in the University of Michigan's Mud Lake Research Area in southern Michigan. Seven habitats (old field, hardwood swamp, bog mat, spruce-birch-larch swamp, spruce burn, oak-hickory upland, and marsh) within the area were selected for study. In addition, six transects were established to cross as many types of habitat as possible. The study areas and transects are described in detail elsewhere (Getz, 1961a, b).

Methods.—Three methods of sampling the abundance of small mammals were utilized. (1) A rectangular study area consisting of 75 trap stations placed in a grid pattern with an interval of 12 meters

was established in all habitats except the spruce burn. This latter area was small and contained only 30 stations. Each study area was trapped for two, 3-night periods, one in October to November, 1957, and the other in January, 1958. One trap (snap-traps in all areas except the old field and marsh; these were live-trapped as described below) was placed at each station. (2) The old field (2.5 hectares) and a 4.4 hectare portion of the marsh were marked off in a grid pattern with a 12 meter interval. Each station was live-trapped for 5 nights each month, September, 1957, through September, 1958. All individuals were marked by toe clipping. (3) Six transects were subdivided into 15 "segments" according to physiognomy of the vegetation, type of substrate and its moisture content, leaf litter, and debris (logs, dead brush, and litter). A trapping station was located every 3 meters along each transect. Each station was trapped for 7 nights during the first two weeks of September, 1958. The capture data for each of the 15 segments were converted to a common factor (number of captures per 500 trap nights) for comparison.

Study of the environmental factors.—The factors studied included vegetation (type and physiognomy), cover, moisture (including standing water), temperature, and food. The methods used to study the environmental factors have been described elsewhere (Getz, *op. cit.*).

Statistical analysis.—Those data that lend themselves to statistical treatment have been analyzed by use of the Spearman rank correlation coefficient (Siegel, 1956). In the following discussions the correlation coefficient (r_s) as well as the probability or level of significance (P) from Siegel (*op. cit.*) are given with statements of correlation or no correlation.

RESULTS

Peromyscus leucopus

Vegetation.—The white-footed mouse is characteristic of forested or wooded areas (Burt, 1940; Linduska, 1950; Johnson, 1926; Wetzel, 1958; Jameson, 1949), but is sometimes found in grassy situations (Blair, 1940; Howard, 1949). Burt (*op. cit.*) believed that the individuals found in grassy areas represent young or unsettled animals. Blair (*op. cit.*) found them to be more abundant in such areas during the summer while Howard (*op. cit.*) found them to be more abundant during the winter. Burt further stated that it may avoid those areas in the forest that have a grass stratum. Linduska (*op. cit.*) also gave evidence to support the avoidance of grassy sites within the wooded areas.

In the present study, *P. leucopus* was limited primarily to areas containing trees or shrubs (Table I; Figs. 1 to 5). (Note. The transect data from the oak-hickory are probably biased. Almost all resident animals were removed when the area was trapped in November, 1957, and January, 1958. Since this area is ecologically isolated from other forested situations, it is possible that the population had not recovered by the time of the transect trapping.) The small number

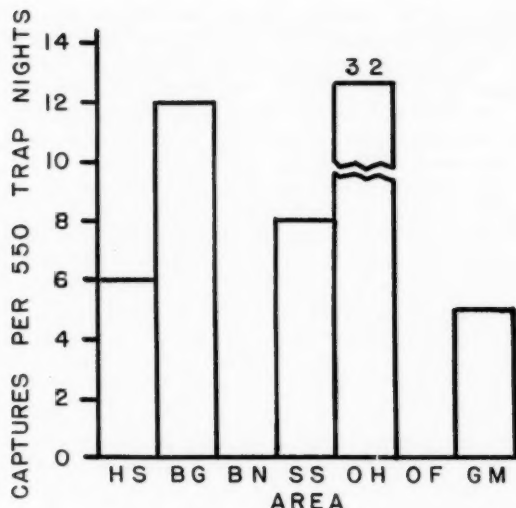


Fig. 1.—Relative abundance of *Peromyscus leucopus* in seven habitats. Fall and winter trapping data combined. HS, hardwood swamp; BG, bog mat; BN, spruce burn; SS, spruce-birch-larch swamp; OH, oak-hickory upland; OF, old field; GM, grass-sedge marsh.

captured in herbaceous vegetation as well as on the bog mat can in most cases be attributed to animals moving from one woody area to another or to the foraging of the individuals for short distances into nearby non-forested areas. However, those individuals occurring in the marsh during the winter (Table I) were not "wandering", but became established for at least two to three months; also they all were adult individuals. Although the area in which they occurred was small, there was an indication that home ranges were established. During the remainder of the year, the individuals captured in the marsh were obviously only moving through the area.

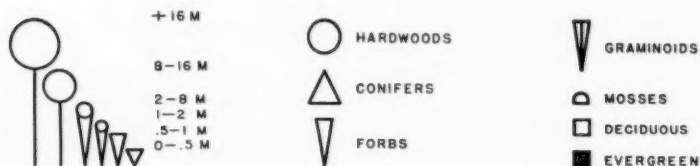


Fig. 2.—Symbols used in the structural diagrams in Figs. 3 and 4. Modified from Dansereau, 1957.

The vegetation of one portion of the marsh (0.8 hectares) consisted primarily of *Potentilla fruticosa*. This species, while having a physiognomy similar to that of a low (0.5 meter) forb, is woody. This area was not inhabited by *P. leucopus*.

That trees are not necessary for the presence of *P. leucopus* was

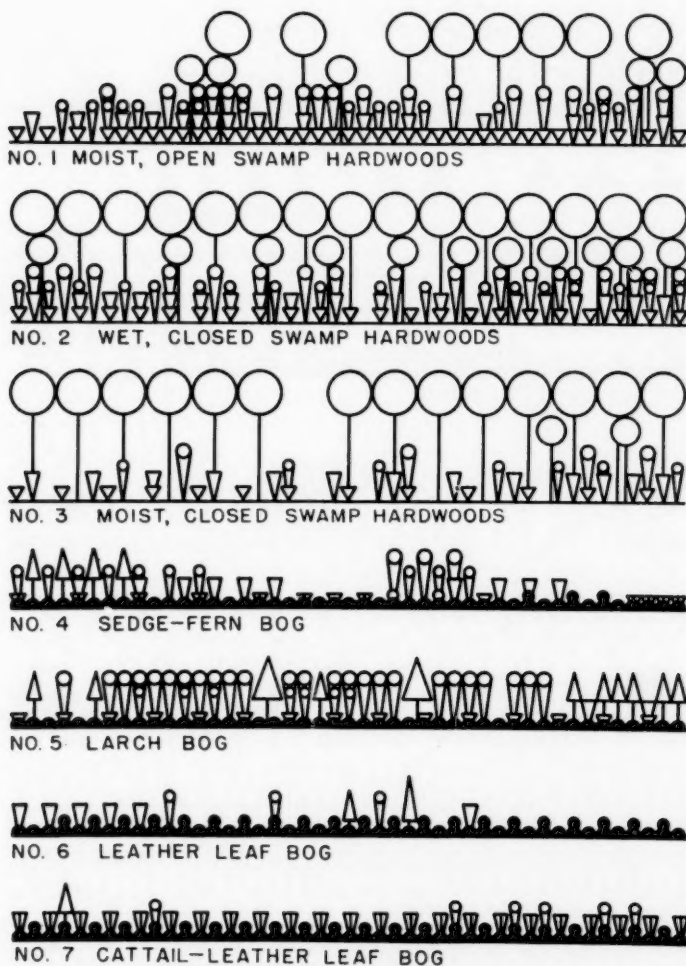


Fig. 3.—Structural diagrams of the vegetation from transect segments No. 1 to 7.
See Fig. 2.

indicated in the *Cornus-Populus* stand in the marsh. This stand consisted of a dense stand of *Cornus racemosa* (2.5 to 3 meters tall) and a few small *Populus tremuloides* (5 to 6 meters tall). At least one or two individuals were present in this site throughout the year (some

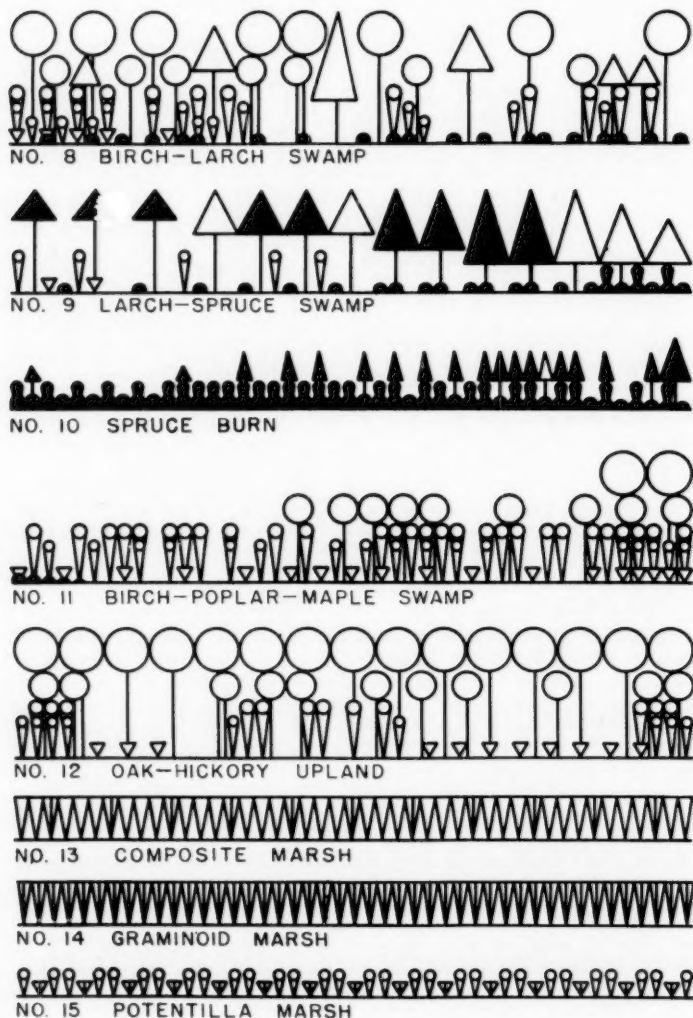


Fig. 4.—Structural diagrams of the vegetation for transect segments No. 8 to 15.

were present in the area for several months so "wanderers" alone were not involved).

Presence of a field or shrub stratum in a wooded area had no apparent influence upon the local distribution of *P. leucopus* as it was abundant in areas where they were present as well as those without such strata (Fig. 5). During the September, 1957, trapping period, 12 live-traps were set in an old pasture adjoining the old field. The traps were in an area in which the vegetation consisted of scattered oak and hickory trees and *Poa pratensis*. Three *P. leucopus* were captured in 5 days of trapping. The nest of a pair of white-footed mice was found under some debris in this site in May, 1958. Observations of acorns and nuts that had been eaten by mice during the period of the study indicated at least a few *P. leucopus* to be present during most of the year.

Cover.—Brand (1952) found that *P. leucopus* is most abundant in areas (within an oak-hickory stand) in which much cover in the form of a shrub stratum or fallen trees and debris is present. In the present study there was no correlation between the amount of cover (in the form of logs, brush, and other debris) in the various habitats

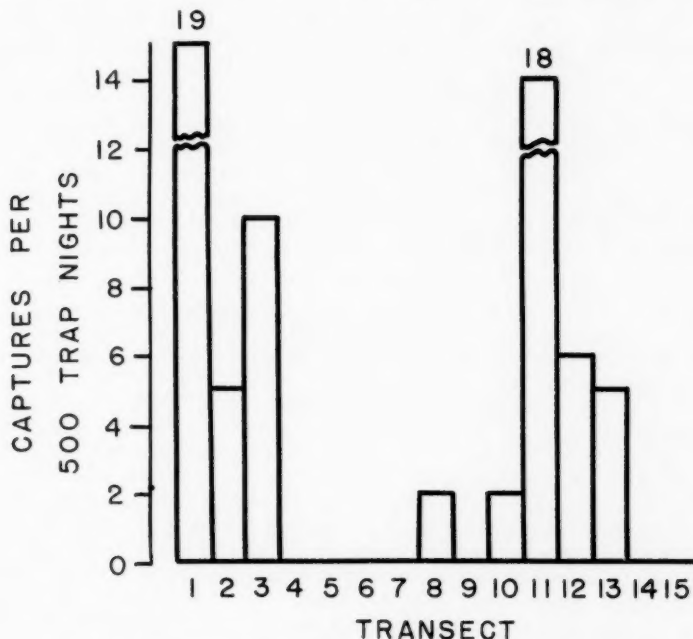


Fig. 5.—Transect captures of *Peromyscus leucopus*. Captures in No. 12 biased (see text).

and the abundance of *P. leucopus* (r_s , .07; P , .05 = .714). Cover of this type was, therefore, not the major factor in the selection of a particular habitat.

Moisture.—Both upland hardwoods and swamp hardwoods have been listed as favorable habitats. Layne (1958) found *P. leucopus* to be particularly abundant in low, swampy woodlands in southern Illinois. Enders (1930) stated that it was able to accommodate to a greater range of moisture conditions than any other rodent. Nicholson (1941) found that few individuals lived on the ground during the summer; they were living and nesting primarily in the trees. This would tend to reduce the influence of excessive moisture or standing water upon the local distribution of *P. leucopus*.

McCarley (1954) found, in Texas, that when *P. leucopus* occurred alone it was present both in uplands and lowlands. When sympatric with *P. gossypinus* (a closely related species), it was found only in the uplands. This may indicate that the upland hardwoods are more favorable for *P. leucopus* while the lowlands are marginal habitats. The reasons for such a distribution were not indicated, however.

A definite negative response to excessive moisture was not noticed in the present study. They were less abundant in the swampy areas, but this may in part be a response to a lesser available food supply (see below). Transect segment No. 2 in the hardwood swamp, which was lowest and contained water during the spring and early summer, had fewer captures than the other two, slightly drier, segments of the hardwood swamp (Nos. 1 and 3). Likewise, those individuals captured during the grid trapping of the hardwood swamp were taken from the higher portion. The wetter segment of the transect was located in a narrow portion of the hardwood swamp (about 50 meters wide, Getz, 1959a); it, therefore, drew its animals from a

TABLE I.—*Peromyscus leucopus* captures in a grass-sedge marsh (1290 trap-nights each month); September, 1957 to September, 1958

Month	No. captures	Average capture per individual
September	2	1.0
October	12	1.3
November	21	1.3
December	17	1.1
January	47	3.0
February	25	2.5
March	13	2.1
April	1	1.0
May	1	2.0
June	0
July	3	1.5
August	3	1.5
September	13	1.3

smaller area. This quite possibly biased the data and gave the impression of few numbers present in such a situation. Because of this and owing to the tendency of *P. leucopus* to be somewhat arboreal, I do not believe excessive moisture to be the primary factor in their avoidance of the wet areas.

Food.—Food of *P. leucopus* consists primarily of seeds, nuts, and acorns (Cogshall, 1928). Fleshy fruits are utilized in season. Insects and other invertebrates have been recorded, but do not appear to form a major part of their diet. Cogshall (*op. cit.*) concluded that food is probably not an important factor in limiting the local distribution of *P. leucopus*. She referred to the species of food plants present and not to the abundance of food in any particular area. Lindeborg (1941) speculated that food availability may influence fluctuations in population densities of *P. leucopus*. Bendell (1959) gives data that show food to be an important factor in regulating population sizes of the white-footed mouse.

In the present study food appeared to be an important factor in the local distribution of *P. leucopus*. This species was scarce in those areas having a lesser stable year-round food supply. From the lists of the more abundant plant species of each area (Getz, 1961a, b), the oak-hickory is most favorable in regards to having a year-round food supply. While species such as *Acer rubrum*, *Vaccinium corymbosum*, *Maianthemum canadense*, and *Rubus pubescens* (which occurred in the swampy areas) may yield an abundant supply of food at certain seasons, their seeds are not as available for later use as are the acorns and nuts of oaks and hickories. These latter trees are most abundant in the upland areas. The presence of such a food supply probably is a major factor enhancing the numbers of white-footed mice in the drier areas while limiting the numbers in the moist and wet areas. Acorns and nuts are utilized the year round as shown by the freshly eaten remains of such items in the oak-hickory at all times of the year.

The spruce-birch-larch area, and especially the spruce portion, which was particularly low in available food, was almost entirely avoided (Figs. 1 and 5). Fallen trees, debris, and shrubs appeared to be as abundant as in other areas that were utilized. Transect segment No. 8 (in the birch-larch stand) was somewhat higher and drier than segments Nos. 1 and 3 of the hardwood swamp. *P. leucopus* captures were much higher in the latter segments, however (Fig. 5). A less available food supply during the fall, winter, and spring seems to be a most likely reason for such results. Similarly the number of captures from segment No. 1 of the hardwood swamp, in which there were a few oak trees (*Quercus macrocarpus*), were higher than from segment No. 3 in which oak trees were absent. This, too, may be a response to a greater food supply in segment No. 1, although the amount of cover is also greater in No. 1 than in No. 3 (Getz, 1961a). Both factors may, therefore, be operating to increase the number of white-footed mice in segment No. 1.

Temperature.—Dice (1922) showed that, under experimental conditions, *P. leucopus* was able to live at a temperature of 0°C in a saturated air with no noticeable ill effects. Sealander (1952) found that *P. leucopus* could tolerate temperatures from $+35$ to -25°C . It was also found by Sealander (1951) that this species may become acclimatized to lower temperatures in the winter and to higher temperatures in the summer. He further concluded (1953) that behavioral responses (burrowing, huddling, and nest building) may allow the animals to survive the effects of air temperatures below those to which they are acclimatized. Such reactions as these would tend to diminish the effects of temperature upon local distribution. Hatfield (1938) found *P. leucopus* to be less active on cold nights. This indicates a behavioral response resulting in the avoidance of excessively low temperatures.

Temperatures had no obvious influence upon the local distribution of *P. leucopus* in the present study. Temperature data obtained in the various areas (Getz, 1961a, b) show that extremes beyond those tolerated by *P. leucopus* did not occur in most habitats. In other areas such extremely low temperatures were of so brief a duration that the animals could survive by seeking shelter in their nests. The white-footed mouse could therefore, tolerate or avoid the low extremes encountered in the various types of situations. That low temperature did not greatly affect *P. leucopus* was indicated by observations obtained from examining tracks in the snow after one of the coldest nights of the year (4 January 1958, which had a surface temperature low of -20°C). A light snow had fallen the evening before and all tracks observed were made during that night. *P. leucopus* had been quite active as had other species of small mammals. If not affected to the extent of being inactive at this low temperature, it seems doubtful that low temperatures could influence their local distribution. The variations in the low temperatures in the hardwood swamp, spruce-birch-larch swamp, and the oak-hickory upland were not great enough to be deemed an important factor in the presence or absence of *P. leucopus* in these habitats.

Since the white-footed mouse is almost entirely nocturnal in habits (Johnson, 1926; Behney, 1936; Getz, 1959b), it is not normally exposed to the higher temperatures. High temperatures are, therefore, probably not a major factor in its local distribution.

Interspecific competition.—Nothing was observed to indicate that other species had an influence upon the distribution of *P. leucopus*. As discussed above, several white-footed mice moved into the marsh during the winter. This site also supported as high a population density of *Microtus pennsylvanicus* as any other portion of the marsh (Getz, 1961b). The two species occurred together for several months with no noticeable effects. Evidently no serious competition occurred.

Conclusions.—*P. leucopus* occurs in wooded areas and does not permanently inhabit those predominantly herbaceous. Under certain circumstances, however, they are found in the latter types. This is

especially true of those individuals moving from one wooded area to another or of those unsettled animals in search of a suitable habitat. There may also be some movement from the wooded areas into nearby grassy areas during the winter. The reasons for such a movement have not been explained.

Within a forested area (other factors being suitable) *P. leucopus* tends to inhabit those sites which contain more fallen trees, dead stumps, and other debris. Likewise, the presence of a shrub stratum also results in higher population densities. The presence of logs, debris, and shrub strata does not influence the selection or avoidance of a particular type of wooded habitat, however. In the present study some areas with many fallen trees and other debris were avoided while others with relatively less cover had high population densities of *P. leucopus*. Those areas with a field stratum of grass-like vegetation may be avoided, but a stratum composed of forbs is not avoided. Likewise, during the winter several individuals lived in a grass-sedge marsh for several months.

The present study revealed no explanation for the occurrence of *P. leucopus* primarily in woody vegetation. An avoidance of a particular type of vegetation as in the case of *Microtus pennsylvanicus* (Getz, 1961b) does not appear to be a factor with *P. leucopus*. Rather, it would appear that there is some positive response to a woody type of vegetation. Food does not appear to be such a factor in their apparent preference for wooded areas as the seeds from many of the forbs in herbaceous areas are readily utilized and are capable of being stored. The individuals that moved into the marsh during the winter utilized the seeds of the forbs that grew in this habitat. Wetzel (1958) believed the preference for habitats with trees is "psychological" in nature or a result of a well-developed climbing ability. The occurrence of the white-footed mouse primarily in wooded areas may in part be explained by its well-developed ability to climb (Horner, 1954). In the present study it did not occur in an area in which the vegetation, while woody in nature, had a physiognomy similar to that of forbs rather than one of trees or shrubs. This tends to support the statement concerning climbing ability. Nicholson (1941) found that *P. leucopus* nested primarily in trees. Whether this is merely a result of the utilization of the type of nest sites available in the forested habitats or an indication of preference for areas having such nest sites has not been demonstrated.

There were higher densities in the drier areas in comparison with those that were wet (i.e., swamps). Although determination of the primary factor involved was not possible, moisture alone does not appear to be the major cause of avoidance of wet areas. Those low areas not having trees such as oaks, hickories, or other nut producers, would not be apt to have a year-round food supply. It appears from consideration of the data obtained in this study that the amount of food available was the more important factor. Excessive moisture may be a contributing factor, however.

As stated above, the amount of available food is an important factor in the local distribution of *P. leucopus*. Those areas that furnish a year-round food supply are able to support higher population densities than are those in which the food supply is abundant, but seasonal.

Surface temperature lows in this study did not vary greatly in the forested areas. Although rather low temperatures did occur at times, seldom did they exceed those that *P. leucopus* is capable of tolerating. Owing to the acclimatization of *P. leucopus* to low temperatures in winter, this factor probably is not important in its local distribution. Should excessively low temperatures occur for short periods of time, behavioral responses such as retreating to nests, huddling, shivering, etc. are sufficient heat conserving mechanisms to allow the animals to survive. The nocturnal activity pattern of the white-footed mouse keeps it from being exposed to high temperatures. High temperature, therefore, is not an important factor in the local distribution of this species.

No influence upon the local distribution of *P. leucopus* by other species was noted in the present study. In regions in which more closely related species also occur competition may result in its being restricted to certain situations (e.g., upland hardwoods).

Zapus hudsonius

The jumping mouse occurs primarily in moist areas (Burt, 1948; Gunderson, 1950; Sheldon, 1938; Goodwin, 1932; Quimby, 1951). Goodwin (*op. cit.*) also found it in dry areas some distance from water. The above papers do not indicate that *Z. hudsonius* is restricted to any particular type of vegetation. It has been recorded from all types ranging from upland hardwoods to bogs and grassy areas. *Z. hudsonius* hibernates during the winter months and thus is not subjected to extremely low temperatures.

Although only a small amount of data was obtained concerning the jumping mouse, a few general conclusions can be made in regard to its local distribution.

Vegetation.—The type of vegetation did not influence the local distribution of *Z. hudsonius*. It was captured in all major types of vegetation except the spruce-birch-larch swamp and oak-hickory upland (Fig. 6). Numerous individuals were captured in the marsh in live-trap stations immediately adjoining the oak-hickory uplands so it seems probable that they were present in this latter habitat also. Owing to the small amount of data it cannot be determined if the absence from the spruce-birch-larch swamp had any significance.

Data from the old field clearly showed that the jumping mouse avoided the inner part of the old field where the vegetation was more sparse. All captures were from along the southern edge which bordered a small sedge marsh and where there was an abundance

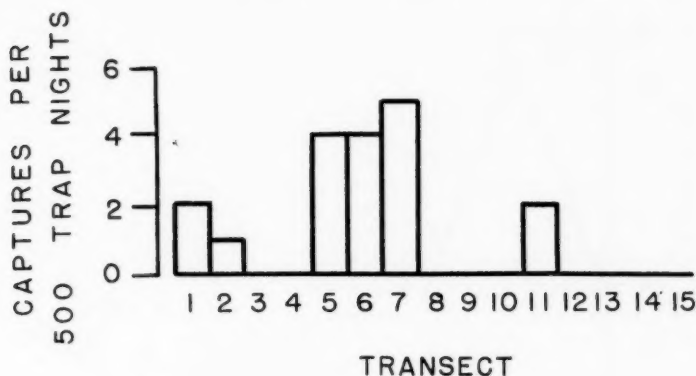


Fig. 6.—Transect captures of *Zapus hudsonius*.

of grasses and shrubs. This can be attributed either to modification of temperature and/or increased moisture. Data from the marsh showed no relationship between amount of vegetation and abundance of *Z. hudsonius*.

Moisture.—*Z. hudsonius* was found exclusively in moist or wet places. As mentioned above, all captures in the old field were from the more moist areas immediately adjacent to a marshy situation. Data from the marsh (Fig. 7) indicate a slight preference for some standing water although there were fewer captures at those stations with more than 2.5 centimeters of standing water. The transect data showed the most captures on the bog mat which was wet. As a hibernating species, it obviously must pass the winter in the drier areas where the frost line is above the water table. During the remainder of the year, *Z. hudsonius* appears to inhabit the more moist situations.

Food.—Not enough data were obtained to reach any conclusions. This species feeds on green vegetation as well as seeds so that an abundant food supply is available during the spring, summer, and fall. Since the animals are not active during the winter, food probably would not be a limiting factor.

Temperature.—These animals hibernate during the winter and thus are not subjected to exceedingly low temperatures. They avoided the sparse vegetation of the old field which may have been in part a response to higher temperatures. No correlation between temperature and the occurrence of *Z. hudsonius* was observed in the other habitats.

Interspecific competition.—No other species exerted an obvious influence upon the distribution of the jumping mouse. Data from

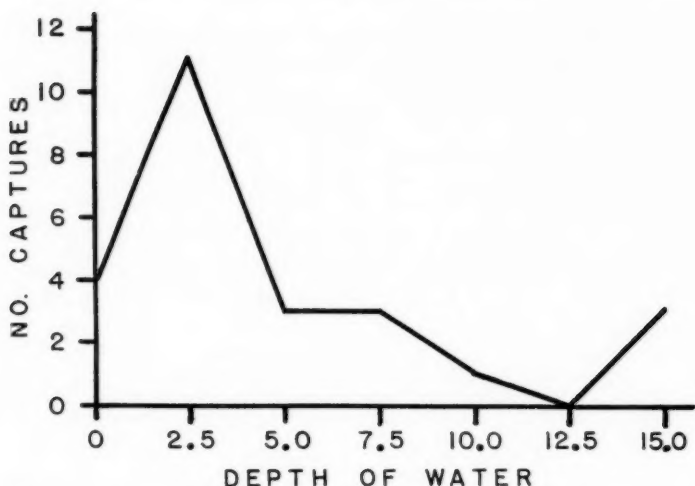


Fig. 7.—Relation of depth of water to captures of *Zapus hudsonius* in a grass-sedge marsh. Water depth in centimeters.

the marsh showed numerous captures at stations that also had numerous *Microtus pennsylvanicus* captures.

Conclusions.—It appears that *Z. hudsonius* occurs only in moist situations. The lowest humidity that it can tolerate has not been determined. In comparison to *Blarina brevicauda* (which has been shown to require an almost completely saturated air; Pruitt, 1959) it is even less abundant in those areas that have low humidities (Getz, 1961a). It, therefore, must be restricted to habitats in which the air is almost completely saturated. Within areas having such a humidity there appears to be no preferred habitat.

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Mating Behavior of the *Peromyscus truei* Species Group of White-Footed Mice

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ABSTRACT: Mice of the *Peromyscus truei* species group (*P. truei*, *P. comanche* and *P. nasutus*) were studied to determine the mating reaction of individuals to members of their own species.

Little intraspecific variation was noted. When the mating pattern was defined, six phases were evident: 1) initiation of courtship by the female; 2) circling of the female before the male; 3) posturing by the female; 4) mounting by the male; 5) thrust-intromission by the male; 6) dismounting by the male.

There is a tendency for pair formation. Interactions such as grooming and genitalia smelling act to condition a mouse to the other's presence, and certain responses, such as the sequence culminating in mating, are given only to those animals with which they have become familiar. Strange animals always elicit responses of an aggressive nature.

INTRODUCTION

This report deals with the results of observations on mating behavior of the species *Peromyscus comanche*, *P. nasutus* and *P. truei* of the *Peromyscus truei* group of mice. These species appear to comprise a natural unit and are presumably genetically more closely related to each other than to members of other species groups. Two species, *P. nasutus* and *P. truei*, are ecologically sympatric over much of their range in mountainous regions of New Mexico and other western states, whereas the allopatric species, *P. comanche*, is limited to canyon floors and slopes of northwestern Texas.

Because of possible differences in mating behavior between the species, attention was focused on observations to determine the mating reaction of individuals to members of their own species. Other purposes of this study were to learn (1) if the female was more important than the male in determining whether copulation occurred; (2) and if she was, at what point in the sequence of mating behavior copulation was permitted.

These observations are presented not as a definitive study but as initial observations on a complicated behavioral sequence, and it is felt that these data should be recorded in the literature, since similar observations have not been reported in any detail.

Acknowledgments.—The author acknowledges John G. Reimann and Alice Louise Baartz for assisting in many aspects of the laboratory work and John A. King and W. Frank Blair for critically reading the manuscript. W. Frank Blair allowed the use of space and equipment in the Vertebrate Speciation Laboratory of The University of Texas, and his cooperation is gratefully appreciated.

METHODS

The mice used in this study consisted of first-generation laboratory descendents of field-caught animals trapped in New Mexico and Texas. Most of these mice had been raised in the Vertebrate Speciation Laboratory for at least a year, and none were less than six months of age when chosen for study. Both males and females were isolated for at least 30 days prior to their use in the observations. Mouse pairs were chosen at random from the stocks available and placed in adjoining compartments of a mating cage. These compartments were connected by a removable wooden tunnel covered with wire mesh. The partition between the two compartments and the side walls and roof of the cage were of quarter-inch mesh and allowed the mice to be aware of each other. As the closed tunnel which separated the two compartments was removed only when observations were made, interactions between the two mice were possible only at that time. Food, nesting material and water were supplied in each compartment.

A male was placed in one compartment and a female in the other. As the displacement of an animal into a strange environment may be a stressful experience (see Southwick, 1959), the usual procedure was to keep the mice in separate compartments for a minimum of 48 hours before observations were begun. Agonistic reactions and excessive motor activity were the usual behavioral responses if they were permitted immediate physical contact. These behavioral reactions were minimized if both mice were given time to adapt to the new environment and become accustomed to the other's presence.

The observational procedure was as follows. The room was darkened at night 30 minutes or more before observations were begun. This period of time was sufficient for the mice to emerge from the nesting material and commence normal nocturnal motor activities. A reflector lamp with a 40 watt red darkroom bulb was placed over the compartments of the cage to be observed, and the observer sat approximately 4 feet from the cage. Although the extent was determined by the behavior of the mice, observations were usually made for a minimum of 20 minutes.

Observations were usually begun at 10:00 P.M. and repeated at one to two hours intervals until copulation was seen. If copulation was not observed by the seventh night, the mice were removed from the cage and replaced by another pair. Clark (1936) reported that

TABLE I.—Mating data obtained in intraspecific pairings of three species of the *Peromyscus truei* species group

Species	Total pairings	Successful pairings	Mean no. of mounts	Mean no. of thrusts	Thrusts per total mounts	Mean no. washings by male	Observation time (in minutes)
<i>comanche</i>	4	2	37.5	31.0	82.7	29.5	190
<i>nasutus</i>	1	1	29.0	25.0	86.2	21.0	85
<i>truei</i>	9	2	10.5	10.5	100.0	8.0	77

the estrus cycle of *Peromyscus maniculatus* females was approximately every 4 to 6 days and that females exhibited breeding condition once during each estrus cycle. Therefore 7 days was considered sufficient to observe estrus if it was to occur.

Fourteen pairings with the 3 species were made, but in only 5 of the pairings was mating behavior seen. Subsequent to each observation a complete account of the behavior of each mouse was recorded. Notes included number of mounts, number of thrusts and washings of the genitalia by the male. These data are summarized in Table I.

GENERAL MATING PATTERN

The mating behavior of the mice in intraspecific pairings was so similar that a general description can be given which is applicable to the three members of the group.

If the female was not in estrus, exploration of the cages was the initial activity after the lights had been extinguished and the tunnel between the compartments had been removed. The mice usually showed no animosity toward each other after a few preliminary encounters and tended to accept the other as a normal component of the environment. Although there was considerable variation between pairs of mice, such activities as mutual grooming and smelling the genitalia, rump and tail of each other were the most frequent interactions.

In several pairings the male appeared to be sexually stimulated when allowed access to the female and would follow and attempt to mount her. If the female was not receptive, she responded in one of several ways. Most frequently she would change to a *defensive posture*, i.e., rear on her hind feet and face the male, her head thrown back and her forepaws held toward her chin. When this posture was taken, the male usually desisted in his efforts and began to explore. Occasionally a female was seen to rotate her body toward the male and snap her jaws toward him. This was frequently accompanied by a short lunge in his direction, and the male would immediately decamp. Not infrequently she would chase him into the adjoining compartment, then resume her investigative activity. If the male was unusually aggressive, these measures were not effective, and she would decamp. Then the male would follow, and a heated chase of short duration would ensue. However, this response was not often observed and was seen only if the male was persistent in his attempts to mount or to smell her genital region.

When the female was in estrus and receptive to the male she placed herself demonstratively before him and initiated a display which normally resulted in copulation. This can be described in the following manner. After the initial contacts between the two individuals had been made, the female evidenced her interest in the male by persistently smelling the scrotum and the base of his tail. The male then turned and smelled the female's genital region. This resulted

in the animals walking in tight circles, their noses to the genital region of the other. After moving in this manner for a short while, the female would then turn away from the male, lower the posterior portion of her body to the floor, and move in tight circles around or in front of the male. In this *circling* display the perineal region of the female was placed in direct contact with the floor of the cage, and the female propelled herself across the floor by movements of the forelimbs. Although in normal locomotion the tail of the animal is held high, the tail of the circling female was held flat to the floor.

If the male was still stimulated, he would follow the female, keeping his nose to the base of her tail or dorsum. Occasionally he might interrupt to smell the floor where she had immediately passed but shortly thereafter would begin to follow her again. The amount of circling by the female varied, but interrupted clock-wise and counter clock-wise movements were common.

Immediately prior to the first copulation the female would cease to circle, extend her body forward and arch her back. This arching was pronounced and usually accompanied by an angling of the tail laterally at its base. Thus the female perineum was raised, and the male would approach from the rear and mount. He extended his body over the female and firmly grasped her in the region of the diaphragm with his forelimbs. Intromission was effected, and at the time of thrust usually one or the other of the male's hind limbs was elevated 2 or 3 millimeters above the floor. Mating was accomplished with a single piston-like stroke of the penis, occasionally of such vigor as to cause the female to lurch forward. Frequently the female was heard to utter a high squeak at the moment of thrust.

After the pelvic thrust the male immediately relaxed his grasp on the female. Then he would throw himself back on his hind legs and tail and begin rapidly to wash the penis, which was withdrawn from the sheath. Washing of the genitalia by the male was regularly but not always seen after each copulation. Although the female *Peromyscus* might wash her perineum after copulation, she most frequently would circle before the washing male, emitting high shrill squeaks as she circled.

Although the frequency and time lapse varied, the duration of union was approximately 0.5 to 2.0 seconds, with shorter periods the most common. Matings occurred rapidly in series from 3 to 10, with the male pausing to groom or rest after each series. During estrus the sex drive of the female rarely lessened, and although the male may have been washing or resting, she would continue to circle before him. The time spent observing the mating pairs was not constant, but as few as 21 and as many as 62 copulations were seen in intra-specific matings. Unless the sex drive of one or the other of the sexes diminished, it was believed that mating occurred at least erratically through the period of darkness until dawn. Mating by one pair was observed as late as 4:45 A.M. when the light of the rising sun began to weakly illuminate the room.

DISCUSSION

When courtship and mating data of the species of the *truci* group are analyzed, a similar pattern consisting of six rather distinct phases is evident.

The first, initiation of courtship, is made by the female, who approaches the male and provides the necessary stimulation conducive to the arousal of the mating pattern. On occasion the mere physical presence of a female was seen to sexually stimulate a male, but if she were in anestrus, stimuli afforded by the male failed to release a reciprocal response. In the male the copulatory threshold, i.e., the stimulation necessary for copulatory activity, varies greatly. A male with a high threshold will ignore a female, even though she may be in estrus, whereas a male with a low threshold will attempt to copulate with an anestrus as well as an estrus female.

The second phase was not mentioned by Svihla (1930) in his general description of the behavior of several species of *Peromyscus*, nor to the author's knowledge has it been described in more recent literature. This phase, the circling display of the female, may or may not take place prior to the first mating but does occur before subsequent matings or series of matings. As this response is released by the female only in the presence of the male, it may be considered as a means by which the female leaves a trail of her sexual condition for the male. In nature it is possible that she might attempt to leave a long continuous trail; so that any male happening upon it would follow her. In the confines of the small cage this trail laying may take the form of circling. Whether circling in the presence of the male in the cage, or laying a long trail in the absence of the male in nature, the stimulus is probably of an olfactory nature. As none of the observations were conducted in more spacious cages, it is not known if circling by the female would be absent from the pattern or if circling is simply an expression of the small cage.

The third phase is posturing by the female. This is characterized by pronounced arching of the back and exposure of the perineum and is a necessary prerequisite for subsequent phases. Prior to the first mating, the second phase may be absent from the mating sequence and the third phase preceded by the first.

The fourth phase, mounting, is initiated by the male. If the female is receptive, the fifth phase, thrust-intromission, follows and consists of a single, rapid thrust of the pelvis by the male. If she is not receptive, she breaks the pattern by decamping. The duration is determined by the male, and the time needed to complete mating is apparently constant in intraspecific matings of the group. The sixth phase, dismounting, is determined by the male. In all matings observed the female maintained her posture until the male had dismounted.

From his careful study of mating behavior in the white rat, Beach (1944) has tentatively concluded that multiple stimulation rather than any particular kind of stimulation is required for arousal of the mating pattern in the male. In other words a combination of olfactory,

tactile, visual and probably other sensations represent the sexually exciting stimulus leading to mating behavior. Evidence from observations of the *truei* group support this. In several observations the male did not respond to the stimuli posed by the female until olfactory and tactile supplemented the visual stimuli. Of the several stimuli essential for the response culminating in copulation, the olfactory appeared to be most important. In all matings the male did not begin his role in the courtship pattern until he had thoroughly smelled the floor of the female's compartment and particularly the genitalia of the estrus female. After initial stimulation of the male, multiple stimuli are probably responsible for a continuance of the mating performance.

Certain data from these observations indicate a tendency for pair formation. Although the mice were usually hostile to each other during the first few contacts, interactions such as nuzzling, grooming and genitalia smelling appeared to be essential for the establishment and continuance of amiable relations. Once begun, these epimeletic activities were continued and acted to condition a mouse to the other's presence. On several occasions when another male was substituted for the original male, the female invariably responded in an antagonistic manner. If in estrus, she never responded to the new male with any of the posturing movements exhibited previously before the familiar male. Likewise if another male were introduced into the compartment with the pair, he was invariably attacked by the resident male. Individual recognition, and subsequent preservation of pair integrity, may well be a fundamental adaptive mechanism as important in *Peromyscus* as in groups of social animals which are closed to other individuals of the same species (see King, 1954).

Certain differences between the mating behavior of these mice and other rodents are apparent. Calhoun (1956) noticed that in *Mus musculus* the male grasped the female by the nape of her neck with his teeth during the union. Likewise he recorded one copulation which lasted as long as 60 seconds. In his work with white rats Stone (1926) noticed a quivering of the ears in female rats when they were mounted, and Stone and Ferguson (1940) recorded from 4 to 8 strokes of the penis by the male rat during copulation. King (1956) recorded a maximum mating time of 2.06 minutes for C57BL/10 inbred mice and observed that after mounting, the male gave several rapid thrusts, becoming slower after intromission, and then becoming passive, frequently falling over on his side.

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Book Reviews

FLORA VAN NEDERLAND. By S. J. Oostroom. P. Noordhoff, Groningen, Netherlands. 890 pages, 1038 text figures. Fourteenth printing, 1956. Price, bound: f. 11,50, or about \$3, American.

This is a new edition of the well-known Dutch flora by Hendrik Heukels, who died in 1936, now revised by Dr. S. J. van Oostroom of the Rijksherbarium, Leiden. At the beginning of the book, there is an outline, by Professor J. L. Van Soest, of the 11 phytogeographical districts of Holland, followed by a map, and an outline of classification of plant associations. There is also an illustrated glossary of technical descriptive terms.

Among several keys to families and aberrant genera, there is a general key, one based on the Linnaean system, and one for vegetative characters. All are of the bracket type. The main part of the book consists of a combination of keys and short descriptions. Duration, time of flowering, habitat, geographical origin of the species, if not native, and Dutch vernacular names are indicated. All this information is very compactly arranged in a series of continuous keys. Most pages have two-line drawings at the top. Toward the end of the book, there is an explanation of abbreviations of names of authors, with their dates of birth and death, and their nationality, this being followed by two indices, one to Dutch names and the other to botanical names.

Some aspects of the taxonomy in this book are likely to be unfamiliar to most American botanists. Archegoniatae and Gymnospermae are accorded modern phylogenetic treatment, but the sequence of families of Angiospermae is less usual. The sequence begins with Dicotyledons, which are divided into Choripetalae (families 18-98), and Sympetalae (99-137). "Amentiferae" come first, with the families Betulaceae, Fagaceae, etc., following in general the Engler sequence up to Caryophyllaceae, then come Euphorbiaceae, etc., followed by Hamamelidaceae (Fam. 40). Ranunculaceae are the 46th family. Violaceae follow Cruciferae. Guttiferae include Hypericaceae. Rosaceae are kept intact, but legumes fall into two families: Mimosaceae, and Papilionaceae, the latter consisting of the two subfamilies, Caesalpinoideae and Papilionatae. Sympetalae begin with Plumbaginaceae and Primulaceae. Ericaceae and Empetraceae are closely associated. Cucurbitaceae and Adoxaceae are left in the usual position according to Engler. Monocotyledons begin with Alismataceae (so-spelled), followed by Liliaceae, Cyperaceae, Gramineae, and Orchidaceae. The last and presumably most highly evolved and specialized families of Monocotyledons are Sparganiaceae and Typhaceae.

While this book appears to be an excellent practical manual for study of the flora of Holland, the underlying system of classification, not original in this book, leaves much to be desired. It is far from phylogenetic, and could, in fact, be termed retrogressive. It is a very dubious improvement over the archaic but familiar Englerian scheme, and in the Dicotyledons at least, is not at all likely to supersede it.—GEORGE NEVILLE JONES, University of Illinois.

ORCHIDS OF PERU. By Charles Schweinfurth. Fieldiana: Botany, volume 30, number 1, 260 pp., 45 text figures, 1 map. Published by Chicago Natural History Museum, April 9, 1958.

This attractive and useful study, by Mr. Charles Schweinfurth, Research Fellow in the Ames Orchid Herbarium, Botanical Museum, Harvard University, is described as the first attempt at a detailed, systematic account of the

orchids of any Andean region. It was prepared in the Orchid Herbarium of Oakes Ames, the largest and most up-to-date of its kind in the world, at the suggestion of Mr. J. Francis Macbride, as part of his comprehensive *Flora of Peru*. Although it is customary to review botanical works after they have been completed, in this instance it may be appropriate and desirable to draw attention to this important monograph in its present stage of publication.

This monograph is based on the collections of pioneer explorers, including Ruiz & Pavon, and on the modern collections of Macbride, Weberbauer, F. W. Pennell, Llewellyn Williams, Killip, A. C. Smith, Ferreyra, Vargas, and several others. These materials have been supplemented by loans of specimens from the Gray Herbarium, New York Botanical Garden, United States National Herbarium, and the Chicago Natural History Museum. Types, or photographs or drawings of types, have been studied from the Lindley Herbarium at Kew, and the Reichenbach Herbarium in Vienna.

Peru is rich in the number of species of orchids, and when all that are known to occur there have been accounted for, there will be about 900 species in 120 genera. The species are arranged alphabetically and described in detail. Many of them are beautifully illustrated by Gordon Dillon. The work includes all binomials attributed to the Peruvian orchid flora, which means that there is a relevant bibliography for each species. Specimens are cited on a definite geographical basis. The framework of the taxonomy is the enumeration of the orchids of Peru (1921) by Rudolph Schlechter. The author modestly attributes the systematic treatment and the theoretical viewpoints implied as having been derived from his long association with the great orchidologist, Oakes Ames. There is also an expression of deep appreciation to his Harvard colleagues, Dr. A. F. Hill, and Dr. R. E. Schultes.

This is a notable taxonomic work, of interest and use not only to orchid specialists, but to botanists and horticulturists in both the New World and the Old. To taxonomists, ecologists, and other students of plants in South America generally, and particularly those of the Andean region, the work is to be regarded as a starting point for further studies of floras of the countries adjacent to Peru. Genera familiar to U. S. botanists include *Habenaria*, *Pogonia* and *Spiranthes*. At least one species, *Habenaria repens*, occurs in southeastern United States, and many others occur in Mexico and West Indies. One statement, that Orchidaceae comprise "between 15,000 and 35,000 members," in the opinion of this reviewer, represents a somewhat generous estimate, but perhaps it is intended to mean that when all species of Orchidaceae have been discovered, described, and classified, the total number will be far in excess of that which we now comprehend.—GEORGE NEVILLE JONES, University of Illinois.

MUSHROOMS OF THE GREAT SMOKIES. A FIELD GUIDE TO SOME MUSHROOMS AND THEIR RELATIVES. By L. R. Hesler. University of Tennessee Press, Knoxville, xii + 289 pp., 183 figs. 1960. \$5.50.

For its many yearly visitors, excluding a certain type of hit and run tourist, the attractions of the Great Smoky Mountains National Park often approach the hypnotic. Some travelers probably see little more than Newfound Gap and Clingman's Dome, which alone are worth the trip. But a surprisingly large number return year after year. The first mistake these perennial visitors make is to get out of their automobiles and walk into the forests. After such an excursion the case is hopeless. Perhaps, a trip through a laurel slick might effect a cure—certainly it almost kills! However, the only successful treatment is to return as often as possible. A surprising number of these visitors

become interested in the flora and fauna of the Park and many become amateur naturalists.

Another kind of visitor to the Park exists. He is the professional naturalist. The majority of these professionals are rightly concerned with their specialties and responsibilities, but on occasion a rare individual may transcend this outlook and try to explain some facet of this fascinating region to its admirers. Professor Hesler is one of these rare professionals. Dr. Hesler's long residence as Professor of Botany and Dean of Arts and Sciences at the University of Tennessee has enabled him to observe the Park fungi in all seasons, and his interest in these fungi, especially the agarics, has been abiding over the years. His guide is a successful attempt to convey to the amateur some of this large store of knowledge.

Many texts aimed at the interested layman often attempt either too much or too little. Professor Hesler has avoided these twin traps. In Part I a brief discussion of the fungi in relation to the Park is presented. The parts of a mushroom are illustrated and discussed along with the properties of edibility and hallucinogenity. Certain phenomena which might confuse or intrigue the amateur such as fairy rings, luminescence, autodigestion, parasitism, and mycorrhiza are also discussed. Part II includes the taxonomic account. One hundred and eighty-three species are treated; an ample number for the beginner. If the amateur's interest is still with him after these, there is appended a short bibliography of available titles to spur him on in his pursuit. Two major keys are included. In the first key are listed the agarics and *Cantharellus*. The conspicuous Ascomycetes, the polypores, the boletes, and *Craterellus* are in the second key. Keys to species are also given. Each of these diagnostic keys are designed to be used with a hand-lens or naked eye, which is an attractive feature to the novice. With a spore-print and fresh specimens, the user should be able to name any of the species included in this guide; a statement which cannot always be made even about keys designed for professional use. By reducing technical jargon to a minimum, that bugaboo is avoided. For that irreducible core of terms there is a short glossary. Each species is excellently illustrated with the author's own photographs and are tastefully arranged to show most of the diagnostic characters. The Kingsport Press is to be congratulated on the reproductions. With each species description there are distributional notes (an inside cover map is included to facilitate discussion), comments on its habitat, and, if necessary, a brief exposition on species with which it might be confused.

While specifically written as a field guide to those mushrooms occurring within the National Park, the book should be useful in adjacent regions. Roughly 25 per cent of the species included in this guide occur even as far south and west as lower Louisiana. The weight, about 1¼ lbs., and dimensions, 8¾ x 5¾ inches, make it easy to carry about in a jacket pocket.

Finally, its dedication to the Park's naturalist, Arthur Stupka, is notably appropriate. Mr. Stupka's knowledge and enthusiasm for Natural History and his vast store of that special kind of patience needed for dealing with amateurs and professionals is immediately recognized by those who come into contact with him.—A. L. WELDEN, Tulane University, New Orleans.

EVOLUTION: ITS SCIENCE AND ITS DOCTRINE. Edited by T. W. M. Cameron. University of Toronto Press (for the Royal Society of Canada). 1960. xi + 242 pp. 24 figs. \$5.00.

This volume consists of twenty papers which were presented at the 1959 meeting of the Royal Society of Canada in commemoration of the centenary

of the publication of the *Origin of Species* by Charles Darwin. Many such commemorative volumes have appeared, but this is among the better ones. The first six papers deal with geological and paleontological aspects of evolution. In the first essay, Russell discusses several examples of polyphyletic ancestry of major groups, and he believes that the establishment of such is one of the major contributions of paleontology to evolutionary theory. In an essay on the Lower Cambrian fauna, Okulitch gives data which show that, contrary to the impressions of many who are not specialists on the Lower Cambrian, the known fauna of the *early* Cambrian was not particularly rich. A highlight of his paper is a brief discussion of the Archeocyatha, an exclusively Cambrian phylum described only a few years ago by Okulitch. As few zoologists are familiar with this phylum, a more extensive treatment would have been welcome.

The next six papers discuss biological aspects of evolution, beginning with an elementary statement of its genetic basis by Thompson. The most original papers in this section are those of Dunbar on the evolution of stability and of Savile on the significance of barrier penetration.

A group of five papers on philosophical and sociological aspects of evolution is headed by the only French paper in the volume, *Quelques Réflexions Philosophiques sur la Science de l'Évolution*, par le R. P. Louis-Marie Régis. Finally, there is a group of three papers on cosmic evolution. Particularly noteworthy here is a paper on the origin of the elements by Cameron, one of the major architects of the current theory of the continuous origin of the elements.

Selection of a few papers for comment from such a series is always difficult. Another reviewer—or this reviewer at another time—might well have chosen quite a different group of papers for comment. The papers are inevitably uneven in interest and readability, but every student of evolution will find much to reward his perusal of this volume.—EDWARD O. DODSON, University of Ottawa, Ottawa 2, Ontario.

THE BIOLOGY OF WEEDS. Edited by John L. Harper. Charles C. Thomas, Springfield, Illinois. 1960. 256 p. Illus. \$9.75.

For the purpose of this first symposium volume of the British Ecological Society weeds have been defined "as higher plants which are a nuisance." This definition, more precise than Emerson's "A plant whose virtues have not yet been discovered" and less laconic than the moralist's "Tobacco," serves to unify a diverse group of plant species of various habits, which in one way or another interfere with human activities. Because of this, the study of weeds has usually been restricted to applied botany, agriculture and control methods; and, as the Introduction to this volume notes, "pure botanists" have avoided these "camp followers of cultivation." The content of this volume explicitly excludes chemical controls from the biology of weeds and except for a few passing references this exclusion has been adhered to, the symposium concerning itself solely with the origins, taxonomy, distribution and ecology, physiology, genetics and evolution of plants which happen to be weeds.

The volume contains twenty-five short papers which are grouped into six sections. The first section, which is not titled includes articles on "The history of weeds in Britain," "Some reflections on the ecology of weeds" and "Patterns of change within grassland communities." The remaining five sections are headed: "Problems in the taxonomy and evolution of weeds,"

"The dormancy and dispersal of weed seeds"; "Population studies, interference and competition"; "Special weed problems" and "Autecological studies on weed species." Most of the authors represent British institutions although several German and one Dutch worker have contributed papers.

While it is not unexpected that the articles included should be varied in quality and interest the general level is good. The topics covered are too varied for easy summarization. Of particular interest in the first section were the late glacial and pre-human existence of weed species and the utilization of weeds as food plants by early man. Some of these are the progenitors of our modern crop plants; others, though used earlier, have fallen from favor and are now outcasts. The observations of H. Lieth of the wanderings of clones within a community in his experiments are striking.

In the second part the attributes of weedy and non-weedy plants are compared and specific taxonomic problems of *Polygonum*, *Viola*, *Hypericum* and *Euphorbia* species considered. The third section includes discussions of the effect of herbicides and root exudates of crop plants on dormancy and germination, the association of weeds and crop seeds, and the effect of husbandry on the seed population. In the fourth section density effects on seed production and population interactions are considered. Specific weeds, *Acacia* in Africa, gorse (known previously to this reviewer only from the misfortunes of Pooh Bear) in New Zealand, water hyacinth in the Sudan and the parasitic *Loranthaceae* in Ceylon are considered in the fifth section. The sixth and last section includes considerations of the autecology of specific weedy species with interesting examples of biological control in polders and the effect of a change in the eating habits of the British public upon the spread of *Nardus stricta* in pastures.

This symposium volume illustrates many fascinating biological problems which are provided by weeds and, however much of a nuisance they may be to the agriculturalist, they should be of great interest to the "pure" botanist.

—ROBERT P. MCINTOSH, University of Notre Dame.

Notes and Discussion

Checklist of American Amphibians and Reptiles

The American Society of Ichthyologists and Herpetologists announces the preparation of a new edition of the Society sponsored *Checklist of American Amphibians and Reptiles*. The new checklist will have a completely revised format with greater detail than any previous edition, will be a loose-leaf publication, and will be authored by many specialists. As the need for revision arises, new individual pages will be published to supplant the original ones. The preparation of the new list is under the guidance of a checklist committee. The chairman and editor is William J. Riemer, Florida State Museum, Flint Hall, University of Florida, Gainesville.

INSTRUCTIONS FOR AUTHORS

In general the author should follow the recommendations of the *Style Manual for Biological Journals* distributed by AIBS at a nominal cost.

Manuscripts should be typewritten, doubled-spaced with ample margins, on one side of 8½ x 11 inch paper. Tables and figures should be placed at the end of the manuscript. Each sheet should be numbered consecutively. The initial page should contain the title, author's name, full mailing address and an informative abstract, not to exceed three per cent of the length of the manuscript. The abstract is published in lieu of a summary. Acknowledgments should be included in the Introduction. Do not underline any words except scientific and generic names.

References in the text should be cited by author and date, e.g., Smith (1960). In the Reference section, they should be listed alphabetically by authors' names. References to periodical literature should contain title, inclusive page numbers and the name of the journal spelled out. Book citations should include author's name, complete title, edition, name and location of publisher, the total number of pages.

A subsidy will be required for papers which exceed twenty journal pages in length and for tabular material in excess of two printed pages. Engraving cost in excess of ten dollars is charged to the author.

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